

PHYLETIC STUDIES OF
TELEOSTEAN FISHES,
WITH A PROVISIONAL
CLASSIFICATION OF LIVING FORMS

P. HUMPHRY GREENWOOD, DONN E. ROSEN,
STANLEY H. WEITZMAN, AND
GEORGE S MYERS

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FOREWORD

THIS PAPER PRESENTS an attempt to assess the main phyletic trends in teleostean fishes, based primarily on study of the living forms. Results indicate the necessity of a major re-grouping of teleostean orders, and this also is attempted.

The work stemmed from talks and correspondence between Greenwood, Rosen, and Myers at the time of and subsequent to the XVIth International Congress of Zoology in Washington in 1963, especially during discussions of the then unpublished results of Greenwood's study of the osteoglossiform fishes and of Rosen's work on the atheriniform fishes (Greenwood, 1963; Rosen, 1964). Active cooperative work was not initiated until early in 1964, when Weitzman joined the group.

The main burden of the investigation has been carried by Greenwood and Rosen, closely followed by Weitzman, who is almost wholly responsible for the strictly ostariophysan lineages and for the stomioid work, and who has also done the figures. Myers has acted principally as adviser and editor, and has contributed in large part to the compilation of the list of family names. Others have helped substantially and are thanked below under Acknowledgments.

Part of the earlier findings of Rosen and Greenwood were communicated orally by them to A. S. Romer, during a conference in London early in 1964, for use by the latter in the new edition of his "Vertebrate Paleontology." That book is still in press at the time we write.

Traditionally, studies such as ours have been based on morphology, especially the skeleton, which is the only complete organ system available for detailed comparison with fossils. However, with the variety of both primitive and advanced teleosts living today, we are most emphatically of the opinion that approaches other than morphological ones would be exceedingly fruitful in the investigation of teleostean interrelationships.

It must be not imagined, however, that the full informational content of teleostean morphology has been extracted, or that it will be fully extracted for a long time. Only the

barest beginnings have so far been accomplished, even within the realm of osteology. We doubt if more than the external anatomy of 95 per cent of the species of living teleosts has been examined, and for many families there has so far been little or no deeper study. Researches on the nervous, digestive, muscular, and vascular systems of teleosts are scattered and mostly uncoordinated, and relatively few of them have been done with any specific systematic objectives in view, despite the fact that pioneer work, such as that of Freihofner (1963) on a single nerve complex, has uncovered a wealth of information bearing upon phyletic relationships.

ACKNOWLEDGMENTS

Many of our colleagues have been exceedingly generous in providing us with information, specimens, and even unpublished conclusions resulting from their own research: Drs. James W. Atz, Reeve M. Bailey, Frederick H. Berry, James E. Böhlke, Charles M. Breder, Jr., Daniel M. Cohen, Bruce B. Collette, Warren C. Freihofner, Robert H. Gibbs, Jr., Messrs. Richard Haedrich, C. M. H. Harrison, Dr. Ernest A. Lachner, Mr. Richard Lund, Mr. Norman B. Marshall, Drs. Samuel B. McDowell, Giles W. Mead, Colin Patterson, Mr. Tyson J. Roberts, Drs. C. Richard Robins, Alfred S. Romer, Bobb Schaeffer, C. Lavett Smith, Victor G. Springer, William N. Tavalga, W. Ralph Taylor, and James W. Tyler.

To Dr. Reeve M. Bailey we are especially grateful for having read through and criticized the entire manuscript and for having provided us with an unusually large amount of original information on the relationships of certain groups and on the validity and orthography of many of the names used in our classification.

For editorial and technical assistance we are grateful to Mmes. Carmella B. Rosen, Marilyn Weitzman, Mary G. Hume, and Miss Victoria Pelton.

We feel that we, as well as all other ichthyologists, owe a debt of gratitude to the late John Roxbrough Norman, for his technically unpublished (mimeographed) "Draft Synop-

sis of the Orders, Families and Genera of Recent Fishes and Fish-like Vertebrates," which we have found to be of the greatest assistance.

The present study was supported in part

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INTRODUCTION

HISTORY

THE LATEST widely accepted general classification of teleostean fishes is that of Berg (1940), and in neither its second edition, edited by Svetovidov (Berg, 1955), nor its German translation (Berg, 1958), is the arrangement of the teleosts materially altered. Berg's teleostean groupings, like those of Jordan (1923), closely reflect the conclusions reached by Regan in a long series of brilliant papers culminating in his brief general exposition (Regan, 1929). Regan's teleostean papers, in turn, were built upon the much earlier foundations laid by Boulenger (1904) and Woodward (1901), and, in the nineteenth century, by Günther, Cope (1871), and Gill (1872, 1893). In fact, except for relatively minor revisions, shifts, and splitting, most of the major groups of living teleosts recognized by Berg do not depart in any revolutionary way from those recognized 70 to 90 years ago by Gill.

In reviewing the literature on fish classification, we were greatly impressed by an almost forgotten scheme proposed by Garstang (1931). Garstang's classification was surprisingly modern in concept and was in effect a rebellion against the rigidity of a taxonomy in which the compartments were artificially arranged and rounded off. In Garstang's own words, a classification consisting of ". . . an array of detached and isolated orders, which conveys no explicit outline of the evolutionary succession . . ." is wrong in that "Its very flatness and lack of relief is indeed a misrepresentation of nature."

More than 20 years ago, Woodward (1942) published a prophetic little paper on the beginnings of teleostean fishes, in which he advanced the view that the Teleostei, long recognized as a natural, monophyletic group, in reality had evolved as a number of distinct

lineages from diverse holostean ancestors in the Mesozoic. Indeed, during the past 35 or 40 years, it has become generally recognized by paleo-ichthyologists that the holosteans themselves represent merely a stage or level of organization into or through which numerous actinopterygian lines passed during their evolution from separate stocks of Late Palaeozoic or Early Mesozoic palaeoniscoid derivatives. Woodward's paper was not widely noted by students of living teleosts, but Bertelsen and Marshall (1956), in discussing the mirapinnids, explicitly supported the view that different teleostean lineages have attained certain comparable grades of organization. The idea of teleostean polyphyletism was expressed by Bertin and Arambourg (1958, p. 2208) in their extensive account of the group. However, their treatment of the living forms appeals to us as chiefly another reshuffling of long-recognized entities, improved here and there by Arambourg's extensive knowledge of fossil teleosts, but marred by an unfortunate lack of familiarity with many Recent groups as well as by such egregious errors as acceptance of Y. Le Danois' (1961) imprecise and unacceptable work on the tetraodontiforms.

Thus we are left at the present day with no general classification of teleostean fishes that has utilized those modern concepts of phyletic classification that have become common in the study of mammalian evolution (e.g., Simpson, 1945). Yet the feeling has been growing among our group and others that many of the most generally recognized teleostean orders are no more than catch-alls for separate lineages which have attained a comparable stage of specialization or complexity (see particularly Gosline, 1960).

THEORY

The problems faced in attempting a "natural" taxonomic classification of a large and varied group of organisms have been widely discussed (see Rensch, 1960, and especially Simpson, 1961). The problems are greatest when the meaningful part of the fossil record is relatively scanty, as it is in the teleosts, and

relationships must be inferred largely on the basis of the morphology of living stocks. The question of "horizontal" versus "vertical" classifications in such groups becomes essentially that of typological versus phyletic taxonomy, which Simpson (1960, pp. 46-66) has adequately discussed.

Teleostean classification, up to and including not only Berg's work, but also a very large part of that of Bertin and Arambourg (1958), has been arrived at primarily by methods that are essentially typological in nature—an attempt first to define orders and other higher taxa and then to speculate upon their origin, albeit in the light of the known fossils. In the mammals, the preponderant weight of the fossil over other evidence long ago forced mammalogists to the phyletic type of classification. No such revolution in teleostean classification has occurred up to the present day.

Of the present authors, Myers has thought for a number of years that the varied "order" of "isospondylous" or "clupeiform" fishes is a polyphyletic assemblage; Greenwood (1963) has already begun the demonstration that such is true; while Rosen (1964 and other work) has begun the dismemberment of Regan's "percomorphs," and the preliminary demonstration of the affinities of certain perchlike groups with the relatives of the salmonoids. Moreover, all of us (see especially Weitzman, 1964, p. 154, and our discussion below on the gonorynchoid fishes) have more recently begun to think that the ostariophysan fishes may be far older than was previously believed and contain separate lineages running back to a generalized Mesozoic teleostean. Our prime purpose, then, has been to separate and point out what we believe to have been the main and subsidiary phyletic lineages of teleosts and the often parallel or converging trends that characterize the evolution of these lines. We have not been especially interested in the definition of living (or fossil) "groups" as such. Definitions of higher taxa, even those based on deep and ex-

tensive study of living assemblages, are rarely very full or precise and are seldom used except by those who wish to emend them.

However, unless one wishes to abandon the principle that taxonomic classification should reflect what can be determined of phylogeny (as some people do), taxa that are obviously polyphyletic must be broken up and a new classification must be adopted.

The classification that we now propose is based on an analysis of what we consider to be the predominant evolutionary trends in the teleosts. By basing the definitions of groups solely on these trends, we have tried to free teleostean classification as much as possible from the confining influences of typology.

This classification is not intended to be definitive at any level. As originally conceived, it was to be nothing more than a series of discussions outlining some new evidence bearing on fish relationships, some new thoughts stemming from the reconsideration of old evidence, and a synopsis of certain outstanding problems. As the work proceeded we realized the need to fill in those areas with which we were not primarily concerned. Indirectly this led to the gradual compilation of a list of family-group and higher taxonomic names. This list, with the subsequent addition of synonymic familial and ordinal names, is included and is intended merely as a nucleus for further search. A series of outline drawings illustrating each of the major families mentioned in the classification is appended.

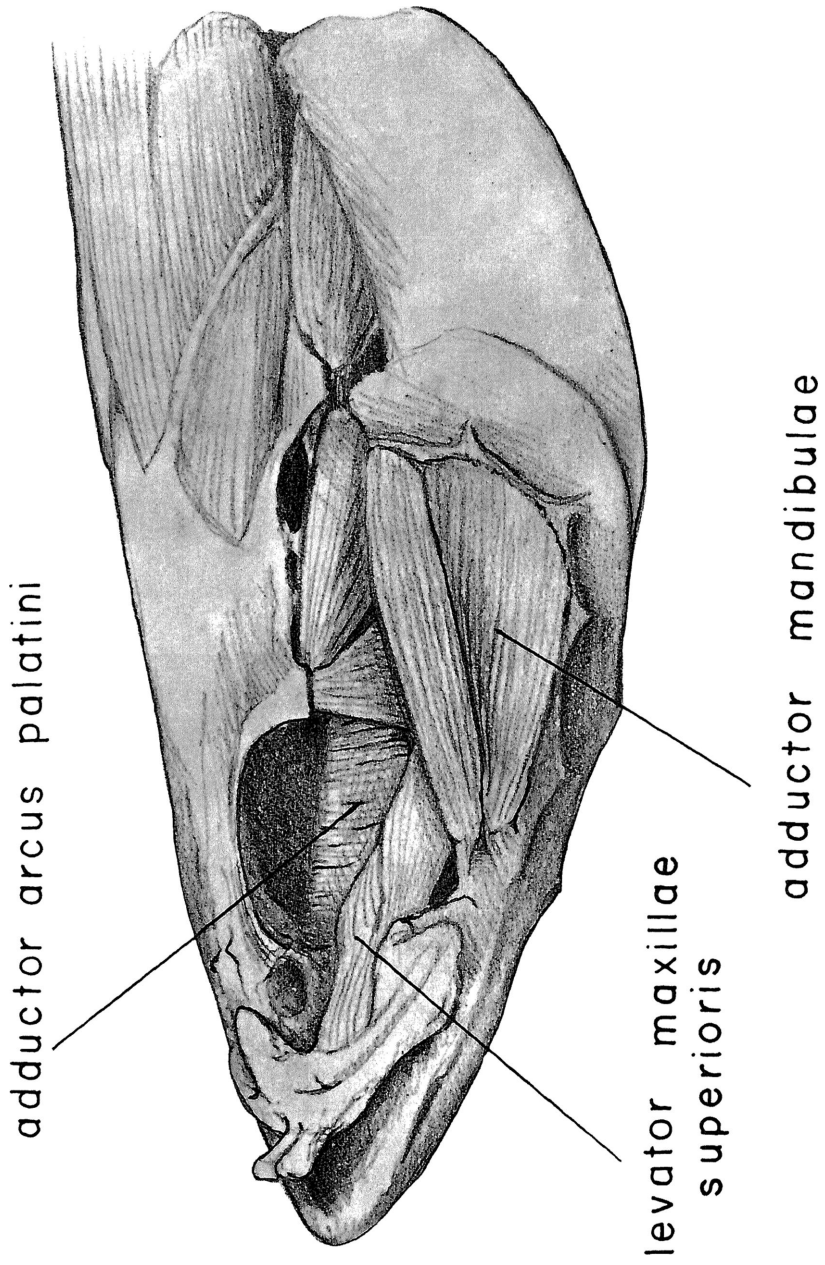
The families recognized, and their placement, follow Berg's (1940) arrangement but with emendations based on works published subsequently and on unpublished information supplied by our colleagues.

TELEOSTEAN DIVERSITY AND AGE

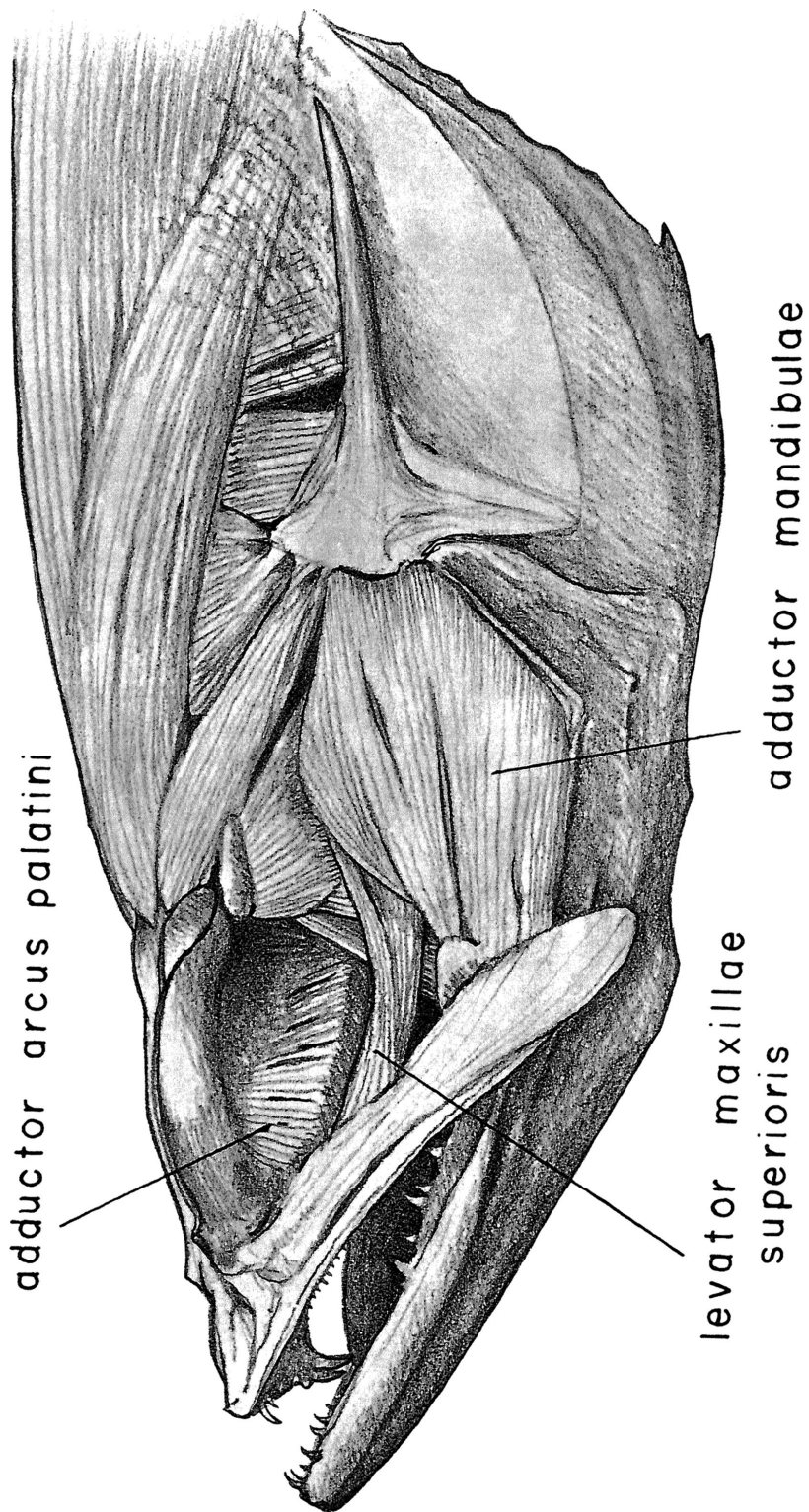
Although the teleosteans are far from being the well-circumscribed group that Johannes Müller (1845) and his successors believed them to be, they are at the present time well separated from the living holosteans and chondrosteans. The term "teleostean" (or "teleost") has meaning, even if it represents merely the final grand stage which so many diverse lines of actinopterygian (or teleostome) fishes have attained, and within

which the actinopterygians have flowered into the largest (hence, by some definitions, the most successful) of all major vertebrate groups.

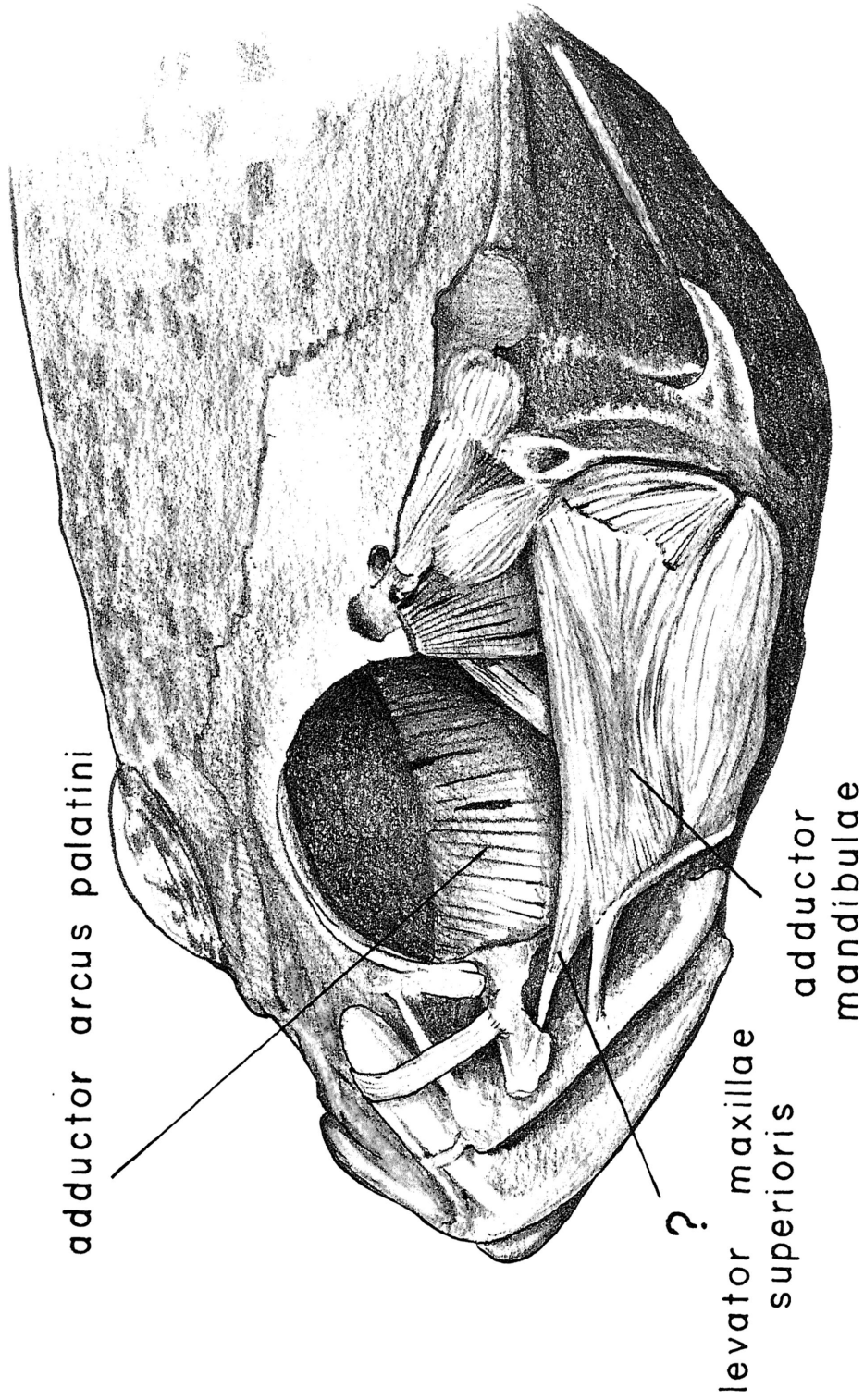
Their diversity is astounding. Estimates of the number of living species vary from somewhat under 20,000 up to 40,000. The facts that discovery of new species and genera is still commonplace, and that new forms of considerable evolutionary importance (e.g.,



Superficial dissection of left cheek muscles of an adult male *Chologaster cornuta*



Superficial dissection of left cheek muscles of *Porichthys porosissimus*



Superficial dissection of left cheek muscles of *Cottus bairdi*. It is unknown at present whether the muscle labeled questionably levator maxillae superioris is actually that muscle in a stage of consolidation with the adductor mandibulae or simply the latter muscle subdivided as in various perchlike fishes

Denticeps and many recently described deep-sea forms) are still being discovered at a surprising rate, demonstrate that we are further from a reasonably complete knowledge of living teleosts than we are of any other large, non-piscine, vertebrate group. Bailey (1960) estimated the present total to be somewhat fewer than 17,000 species, and Myers (1958) estimated that the eventual total number of living species will approach or surpass 30,000. The most numerous additions to the total may be expected in the deep seas and in the excessively rich fresh-water fauna of tropical America.

Unlike mammals, of which most of the living orders had their origin in the Cenozoic and of which extremely few relicts of Mesozoic or early Cenozoic type persist, a considerable number of living teleosts belong to genera close to or perhaps even identical with Eocene, Paleocene, or Cretaceous forms. Also unlike mammals, the number of known living genera and species far surpasses the number of known fossils. For these reasons, a classification based principally on the Recent teleosts, as this one is, has far more validity than would a classification based on Recent mammals, or the Recent forms of other large vertebrate groups.

Fishes of teleostean type (Leptolepididae) first appear in the known fossil record in the Middle Triassic. Some of these are so advanced in the details of their structure that we can speculate that the shift from the holostean to the teleostean level began much earlier in some forms. However, the dearth of Early Mesozoic fossils of teleostean type, except in marine Triassic and Jurassic beds in the area of the Tethys Sea, may be related to a fresh-water origin of many teleostean lines in regions where fresh-water, fish-bearing deposits are rare or undiscovered. The many teleosts known from the deposits of epeiric

seas laid down during the Late Cretaceous indicate that several lineages had by then attained an organization similar to that of living forms. This statement is especially true of the elopoid and berycoid lines. However, the absence in known Cretaceous deposits of several important lines of teleostean development (notably the salmonoids and ostariophysans, which give considerable evidence of an age comparable to that of the elopoids) again leads to the suspicion that much teleostean evolution was going on in Mesozoic fresh waters—evolution of which we as yet have no trace.

By the Eocene, or possibly even the Paleocene, teleostean marine shore-faunas bore a striking resemblance to modern assemblages, a fact that again is wholly unlike the situation in mammals. Since that time, a number of teleostean families appear to have undergone comparatively little change.

Unfortunately, we know comparatively little about Paleogene fresh-water or deep-sea fishes in any part of the world. We may presume that ostariophysan types not greatly different from living forms were in residence on nearly all the continents, a presumption based on some concrete fossil evidence. The appearance of undoubted bathypelagic stomiatoid and myctophoid fishes in Early Neogene records, in which these fishes are of wholly modern type, leads also to a presumption that they, too, arose much earlier.

We have not excluded fossils from consideration, although we do not place them in our formal classification. A number of important fossils are discussed in the expository comments preceding our classification. Paleo-ichthyologists who deal extensively with teleostean fossils are quite aware that the classification of living teleosts must be understood before the fossil record can be properly interpreted.

NATURE OF MAJOR GROUPINGS ADOPTED

ENOUGH IS SAID above about the evolutionary trends exhibited by different lineages to indicate our belief that these lineages often pass through or arrive at similar levels or stages of organization. We propose, for example, that separate evolutionary routes toward the acanthopterygian grade had been traversed by relatively unrelated lines, and we also propose that the malacopterygian level probably was attained polyphyletically from holosteans of pholidophoroid type.

The following series of synopses and discussions outline the reasons for the new alignments given in the formal classification. The principal innovations in this classification are the separation of the teleostean fishes into three divisions¹ and the realignment of taxa among eight superorders (fig. 1). Various smaller groups (suborders and families) are redistributed among orders, both new and old.

In our conception, each of the three divisions represents a distinct phyletic lineage derived from the holostean level of organization. It is presumed that in Division I a primitive elopiform ancestor has produced principally the eels and eel-like fishes and perhaps also the herring-like fishes. However, we know of no evidence to rule out the possibility that the herrings and their allies had an independent origin from among the pholidophoroids. For the present, and because elopomorphs and clupeomorphs appear more closely related to one another than to other groups, we have followed a conventional alignment of these fishes.

In Division II there have evolved only two series of unusually specialized, and predom-

inantly fresh-water, radiations, the Osteoglossiformes and Mormyriiformes. Neither of these orders could possibly have been involved in the ancestry of other teleosteans.

By contrast with the other divisions, Division III contains the bulk of the living teleostean fishes. There have evolved within this division several radiations leading to more than one organizational level and to the dominant groups of extant fresh-water and marine species, namely, the Ostariophysi and the Acanthopterygii.

In the discussions below of the major structural and developmental divisional trends, where we outline the reasons for erecting the various new orders and superorders, a separate analysis is given of the suborders Stomiatoidei and Alepocephaloidei of Division III because of their previous placement near groups here included in Division I. The ordinal and subordinal composition of the superorder Ostariophysi is also given in detail. The one superorder not discussed at length is the Atherinomorpha. It does not fall readily within the concepts of either of two adjoining groups, the Paracanthopterygii and Acanthopterygii, although it includes forms at more or less the same organizational level as the fishes of those superorders. The main structural and developmental characteristics of the Atheriniformes, the only contained order of the Atherinomorpha, were described in some detail by Rosen (1964).

Among the various living primitive groups of teleosteans, only elopids (Division I) and salmonids (Division III) are sufficiently generalized to be suitable morphologically as basal types for the major teleostean radiations. Other primitive groups, for example, the clupeiforms and osteoglossiforms, are too specialized for this role. We realize that elopids, of all teleosts, possess the greatest assemblage of holostean characters. At the same time, we recognize that their larval and other specializations, and the absence of certain snout and jaw structures (see discussions below), put at least the living elopids off the main course of teleostean evolution. Salmonids, on the other hand, have none of these limitations and thus

¹ Parenthetically, we should mention that the possibility of utilizing the methods of numerical taxonomy to help solve many of the major questions of relationships has occurred to us. Our reluctant conclusion has been that the work of encoding (for computer techniques) the at times esoteric (and so heavily weighted) evidence that we have dealt with would not only have violated the weightless spirit of numerical taxonomy, but perhaps have postponed presentation of our results until our respective retirement ages. However, for the benefit of our "numerical" colleagues, we have numbered our major divisions (I, II, III).

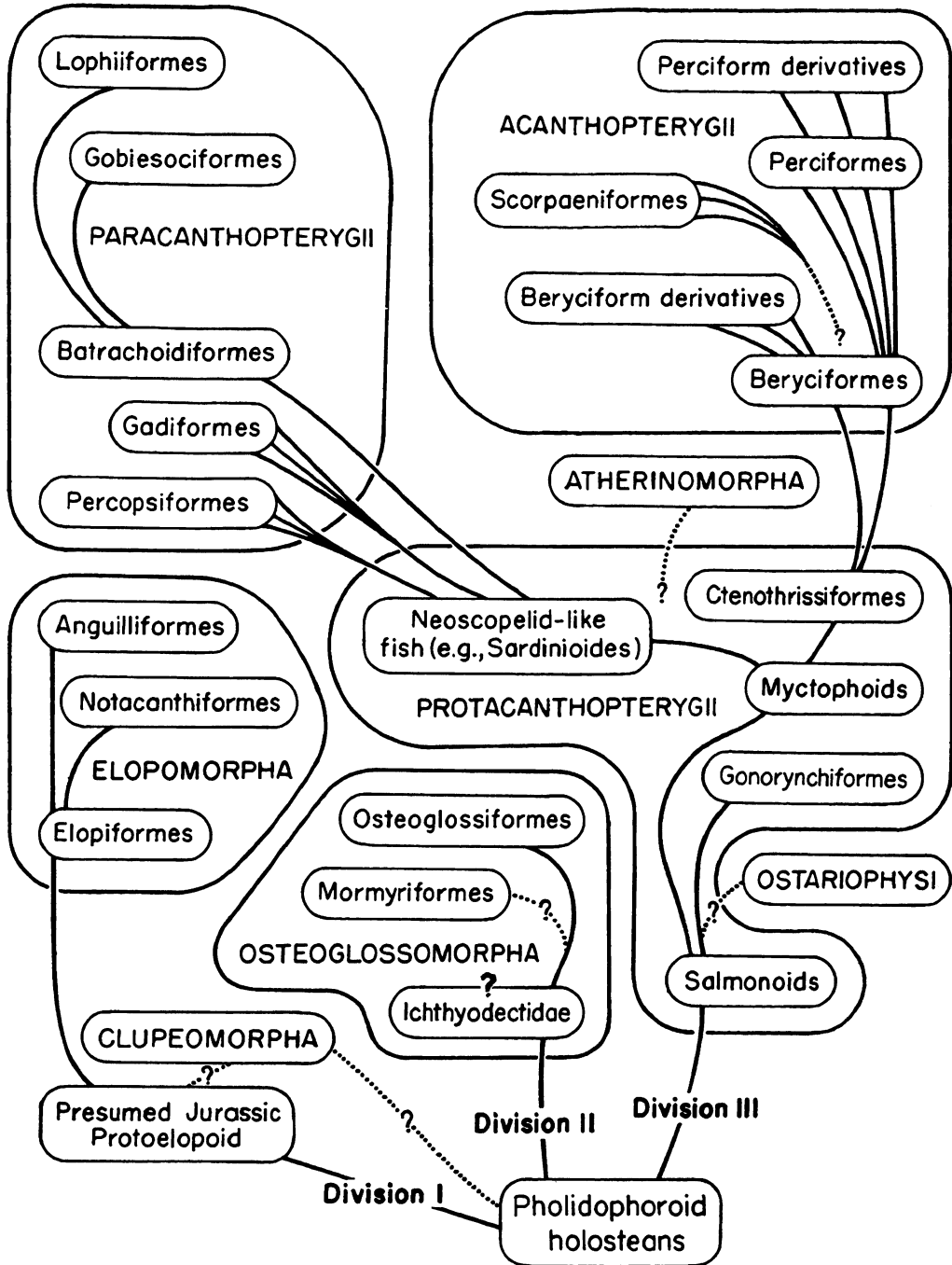


FIG. 1. Diagram showing our conception of the evolutionary relationships of the principal groups of teleostean fishes. Uncertain relationships are shown by a broken line and question mark.

seem better to fulfill the requirements of a morphotype that may have given rise to the major radiations of Division III. A question that naturally arises from this conclusion concerns the possibilities that elopids and salmonids might have arisen polyphyletically from the holostean level or monophyletically from a single holostean or early teleostean entity. Elopids are still so close to the holostean grade, however (indeed, some workers con-

sider them to be holosteans), that a common ancestor of these two modern groups, if it existed, was itself likely to have been an advanced type of holostean fish. If this view is supported by paleontological evidence, as we think it ultimately will be, the salmonids and elopids would represent separate attainments of the teleostean grade and thus would be, *ex hypothesi*, examples of polyphyletism, at least at the teleostean level.

MAJOR TRENDS WITHIN THE DIVISIONS AND SUPERORDERS

DIVISION I

Fishes of ancestry at or near the holostean level of organization in which each contained group except for the eel-like fishes has one or more very primitive members.

Characteristic and often primitive trends include:

1. The development, particularly in the compressed, silvery, marine fishes, of a short, broad, and arcuate maxilla equipped with large movable supramaxillae in association with a high coronoid process on the dentary and articular.
2. The development of maxillary teeth that are seldom excluded from the gape, even partially.
3. The development of parasphenoid and pterygoid teeth.
4. The development in the basicranium of numerous separate intraosseous passages for the parts of the fifth and seventh cranial nerves and certain major blood vessels.
5. The development of a full complement of intermuscular bones.
6. Caudal fin, when present, with hypural supports on one to four centra.
7. The development of a functional ductus pneumaticus.
8. The development of an otophysic connection¹ not involving the intercalation of bony elements.
9. The development of an ethmoidal commissure of the cephalic lateral-line system.
10. The development of a confluence between the preopercular and infraorbital cephalic lateral-

¹ We define "otophysic connection" as the involvement of the swim bladder with the otic region, usually effected through bilateral prolongations of the swim bladder which either come into superficial contact with the cranium in the region of the inner ear or penetrate the cranial wall and form an intimate association with the inner ear intracranially. Exceptionally the swim bladder-ear connection may be effected through a chain of ossicles linking the perilymphatic cavity with the swim-bladder wall.

line canals, hence the formation of a recessus lateralis.

11. The development of a leptocephalous larva.

ELOPOMORPHA

1. Principally marine fishes of diverse form, most of the modern species eel-like.
2. Gular plate in non-eel-like representatives.
3. Branchiostegals usually very numerous.
4. Mesocoracoid arch present only in the non-eel-like forms.
5. Hypurals, when present, on three or more centra.
6. Ethmoidal commissure present or in modified state in many groups.
7. Opercular series often reduced or even absent.
8. Larva, when known, a leptocephalus.

CLUPEOMORPHA

1. Silvery compressed fishes, usually marine, with caducous scales.
2. Branchiostegals numbering as high as 15, but usually fewer.
3. Intracranial diverticula of swim bladder forming bullae within the ear capsule.
4. Mesocoracoid arch invariably present.
5. Hypurals on one to three centra.
6. Cephalic lateral-line canals extending over operculum; usually no lateral-line pores on trunk.
7. Recessus lateralis present.

DIVISION II

Fishes of ancestry at or near the holostean level of organization in which all contained members have retained numerous primitive characteristics of the jaw suspension and shoulder girdle, and have developed complexly ornamented scales.

Characteristically primitive trends, and some of the divisional specializations, include:

1. The fusion of the premaxillae into a single bone.
2. The development of a simple, well-toothed maxilla (edentulous in the Mormyriiformes), generally contributing to the gape but partially excluded in a few genera.
3. The development of parasphenoid, glossohyal, and pterygoid teeth.
4. The fusion of various elements in the palatopterygoid arch, the palatine and vomer fused in Mormyriiformes.
5. The development of paired tendon bones (uncalcified in *Hiodon*) on the second hypobranchial or second hypobranchial and basi-branchial, in all genera.
6. The loss, in many species, of multiple intraso-oseous passages in the prootic bone for the fifth and seventh cranial nerves and certain major blood vessels.
7. A reduction, in two phyletic lines, of the caudal fin and its confluence with the dorsal and anal fins.
8. The development, in those genera with a distinct caudal fin, of a supporting skeleton of which the elements are not readily homologized with similar elements in fishes of other divisions. There is a reduction in the number of hypural elements which are apparently supported by two and a half centra in all except one genus (*Hiodon*), in which three centra are involved and there is a full complement of hypurals.
9. A reduction in size, or loss, of the suboperculum.
10. The development of upper intermuscular bones only.
11. The development of a functional ductus pneumaticus.
12. The development of an otophysic connection not involving the intercalation of bony elements in the young or adults of all groups except the Osteoglossoidei in which no connection exists.
13. The development of distinctly separated preopercular and infraorbital canals and the occurrence in a single genus (*Pantodon*) of a supraopercular bone.
14. The development of somatic electric organs in one order.

OSTEOGLOSSOMORPHA

1. Fresh-water and predominantly tropical fishes of extraordinarily diverse body form and size, and including one form in which the pectorals are greatly expanded so as to give the impression of a flying fish. Most species are insectivorous or piscivorous.
2. Premaxillae ankylosed to form a single median bone in one order (Mormyriiformes) and in one genus of the Osteoglossoidei (*Pantodon*);

the premaxillae firmly bound to the ethmo-vomerine region in all genera.

3. Primary bite of mouth between parasphenoid and glossohyal and basihyals.
4. Head of palatine without maxillary process.
5. Branchiostegals three to five, in two cases 11 and 13.
6. Subtemporal fossae present in only a few genera.
7. Expansive suprascapulars in all except the Osteoglossoidei.
8. A lateral cranial foramen in most species (Osteoglossoidei excepted).
9. Hypurals, in fishes with distinct caudal fins, reduced in number by fusion of the upper elements and, apparently, supported on at least two and a half centra in all.

DIVISION III

Fishes mostly of distinctively teleostean level ancestry, only a single basal group having obviously holostean affinities.

Characteristic trends include:

1. The lowering of the center of gravity and the approximation of the center of buoyancy with the center of mass.
2. The development of a large, frequently mobile premaxilla that completely or partially excludes the maxilla from the gape.
3. The loss of maxillary teeth and functional supramaxillae.
4. The loss of parasphenoid and pterygoid teeth.
5. The development of an os pharyngeus inferior and an os pharyngeus superior and the development of mm. retractores arcua branchialia attached to the third to sixth vertebrae.
6. The development in the basicranium of a common passage (trigemino-facialis chamber) for the fifth and seventh nerves and orbital artery and head vein.
7. Loss of the supraorbital bone.
8. The reduction in size of the infraorbital bones.
9. The reduction in the number of scale bones in the dorsicranium.
10. The loss or reduction of certain temporal fossae but the enlargement of the posttemporal fossa and the loss of its roof.
11. The covering of the posterior part of the dorsicranium by epaxial body muscles.
12. The elevation of the pectoral fin base on the side.
13. The forward migration of the pelvic girdle and its linkage with the pectoral girdle.
14. The reduction in the number of pectoral radials.

15. The reduction in the number of vertebrae and of pelvic and caudal fin rays.
16. Reduction of intermuscular bones.
17. Reduction of the hypural bones to a single unit on a terminal half-centrum.
18. The varied specialization of caudal fin shape.
19. The development of an adipose fin in several primitive lines.
20. The development of fin spines and ctenoid scales.
21. The development of an otophysic connection involving the intercalation of bony elements.
22. The disappearance of the ductus pneumaticus.
23. The development of distinctly separated preopercular and infraorbital canals, hence the frequent occurrence of a suprapreopercular bone.
24. The development along the trunk of a ramus lateralis accessorius of the seventh nerve.

PROTACANTHOPTERYGII

1. Predominantly slender, predatory fishes; many generalized and some specialized forms in fresh water.
2. Photophores in oceanic representatives.
3. Widespread trend toward exclusion by premaxillae of the maxillae from the gape.
4. Widespread trend toward the development of premaxillary processes.
5. Palatopremaxillary and ethmomaxillary ligaments present in numerous representatives.
6. Upper jaw slightly protrusile in a few cases.
7. Glossohyal teeth usually prominent.
8. Branchiostegals very numerous in many instances, reduced to two or three in some cases.
9. Hyoid and branchiostegal skeleton approaching paracanthopterygian and acanthopterygian form.
10. Paired proethmoids present in many cases, often simulating ascending premaxillary processes.
11. Few species with opercular spines or serrations.
12. Mesocoracoid present in generalized lines only.
13. Baudelot's ligament to first vertebra.
14. Occasional trends for the pelvic fins to advance; pelvis commonly of more than six rays.
15. Occasional trends toward elevation of the pectoral fin base on flank.
16. Vertebrae commonly more than 24, pre-caudal elements commonly 15 or more.
17. Hypurals on one to three centra, but a basic acanthopterygian caudal skeleton developed in some representatives and a paracanthopterygian type in others; caudal fin commonly with more than 15 branched rays.
18. Adipose fin present in most species.

19. Suprapreopercular (canal-bearing ossicle above uppermost part of preopercular canal) present in generalized representatives.

OSTARIOPHYSI

1. Predominantly fresh-water fishes of world-wide distribution on the continents and adjoining archipelagoes, of extraordinarily diverse form and habits, encompassing numerous well-toothed predatory and vegetarian types and toothless detritus and microphagous types, many of both categories with well-developed circumoral barbels.
2. Upper jaw protrusile in numerous species.
3. Major trends toward reduction in number (or absence) of jaw teeth.
4. Lower pharyngeal bones usually well developed.
5. Branchiostegals generally few in number but as many as 15 in some species.
6. Pelvic fins abdominal.
7. Hypurals on one centrum.
8. Fin spines present in numerous instances.
9. Scales present or absent, when present cycloid in most instances, ctenoid in a few, and in certain forms replaced by dense, bony plates.
10. Adipose fin in many groups.
11. Otophysic connections involving the intercalation of bony elements in all.
12. Swim bladder primitively subdivided, reduced in many species.
13. Suprapreopercular (ossicle above uppermost part of preopercular canal) in numerous species.

PARACANTHOPTERYGII

1. Mostly marine, stout, soft-bodied fishes inhabiting deep waters or when in shallow water being nocturnal or occurring in cryptic habitats.
2. Virtual loss of photophores.
3. Feeding mechanism adapted for carnivorous diet in all species.
4. Ascending process of premaxilla often joined to premaxilla by flexible cartilage, or absent; premaxilla with an articular process in all cases, and with a lateral (maxillary) process in most cases.
5. Ethmomaxillary and palatopremaxillary ligaments well developed.
6. Upper jaw not protractile.
7. *Mm. levator maxillae superioris* well developed, or modified and consolidated with part of *m. adductor mandibulae*.
8. Superficial division of *m. adductor mandibulae* reduced or absent.
9. *M. adductor arcus palatini* covering floor of orbit.
10. Ceratohyal and epihyal ankylosed.
11. Branchiostegals not exceeding six in num-

ber, the bladeliike elements with an anteroproximal prong in most species; the four bladeliike elements on the outer face of elevated part of hyoid bar, the anterior hairlike elements on the inner side of the depressed anterior section of ceratohyal.

12. Upper and lower pharyngeal bones well developed and toothed.

13. No subocular shelf on infraorbital bones.

14. Extrascapular bones present, often forming solid roof for posttemporal fossae.

15. Parietals meeting in midline or closely approaching one another in most species and frequently housing a posttemporal commissure of the cephalic lateral-line system.

16. Intercalar very extensive in numerous species.

17. Mucous canals prominent on head of most species.

18. Baudelot's ligament to first vertebra, or to basicranium where first vertebra is fused to basioccipital.

19. Modified epipleural ribs ("endocleithra") from exoccipitals to cleithrum in several species.

20. Mesocoracoid absent; pectoral radials two to 13, often hourglass-shaped, very long, and extending well beyond the scapulocoracoid margin.

21. Pelvic fins thoracic, jugular, or mental in all but one species, with occasionally as many as 17 rays.

22. Pleural ribs often reduced, frequently absent.

23. Caudal skeleton, when present, with two large hypurals on separate vertebrae in most, or the two fused together into a single unicentral unit.

24. Fin spines developed or not.

25. Ctenoid scales developed in some species.

26. Swim bladder frequently subdivided and connected by diverticulae to parapophyses of precaudal vertebrae, in some instances an otophysic connection involving the intercalation of bony elements.

27. Numerous species viviparous.

ATHERINOMORPHA

1. Generally small surface-feeding fishes, principally in fresh and brackish water, some marine, most fresh-water species with pronounced secondary sexual dimorphism in size, in color, and in fin shape and function; many species with bony external male genitalia developed from anal, pelvic, or pectoral fin, or some combination of these.

2. Upper jaw protractile in many species, without true ascending processes, and supported by a foundation of loose connective tissue and a complex maxillary process, without palatopremaxillary or ethmomaxillary ligaments.

3. Mm. levator maxillae superioris absent.

4. Superficial division of m. adductor mandibulae present and well developed, with a tendon to the lower maxillary shaft.

5. Upper and lower pharyngeal bones well developed, dentigerous, the upper bones consisting of a large plate made up of pharyngobranchials 3 and 4 and smaller modified pharyngobranchial 2; pharyngobranchial 1 present but obsolescent in only a few instances.

6. Ceratohyal and epihyal joined together by dorsal lamella.

7. Branchiostegals four to 15 in number.

8. Mesethmoid usually bilaminar, invariably discoidal or scalelike.

9. Infraorbital series reduced to two, rarely three, elements.

10. Opercular bones unarmed.

11. Pectoral radials four in number, cuboidal, recessed within excavation in scapulocoracoid margin.

12. Supracleithrum, when present, discoidal, confined within dorsal tip of cleithrum.

13. Baudelot's ligament to basicranium.

14. Pelvic girdle abdominal, subabdominal, or thoracic.

15. Vertebral number high in most species, pre-caudal number modally 20.

16. Caudal skeleton with two large hypural plates of opposite symmetry on terminal half-centrum, with in no instance more than four hypurals, of which two are invariably broad and fan-shaped.

17. Fin spines present or not.

18. Ctenoid scales in relatively few species.

19. Numerous viviparous species, some with unique encapsuled or unencapsuled spermato-phores.

20. In oviparous species, egg large, demersal, with adhesive filaments, and without oil globule.

21. Embryo with heart displaced forward anterior to head.

ACANTHOPTERYGII

1. Fishes of extremely variable form and habits, principally in salt water and principally benthic and littoral.

2. Photophores very uncommon.

3. Feeding mechanisms extremely varied, permitting the utilization of numerous food sources.

4. Upper jaw protractile in many species, with a premaxilla having ascending, articular, and lateral (maxillary) processes.

5. Palatopremaxillary and ethmomaxillary ligaments present, but in some cases modified.

6. Mm. levator maxillae superioris muscle absent in all but one genus (*Polymixia*).

7. Superficial division of the m. adductor mandibulae well developed.

8. *M. adductor arcus palatini* usually confined to posterior wall of orbit.
9. Upper and lower pharyngeals well developed and toothed.
10. Hyoid bar with ankylosed ceratohyal and epihyal; distal, depressed section of ceratohyal with large foramen in many cases; elevated proximal part of ceratohyal and epihyal with four bladeliike branchiostegals, the hairlike anterior branchiostegals, when present, on inner surface of depressed distal section of ceratohyal.
11. A subocular shelf present on the infraorbital series in numerous species.
12. Infraorbital bones frequently in contact with preoperculum.
13. Bones of head commonly with numerous pungent spines.
14. Opercular apparatus armed in many species.
15. Baudelot's ligament usually attached to basicranium, rarely (*Polymixiidae* and some *Scorpaenidae*) to first vertebra.
16. Supracleithrum strutlike, extending above cleithral tip in most members of the group.
17. Mesocoracoid absent; pectoral radials not exceeding four in number, often hourglass-shaped.
18. Pelvic fins, if present, thoracic or jugular in position, pectorals inserted high on the sides.
19. Pelvic fin typically consisting of a spine and five articulated rays except in berycoids and a few other forms.
20. Pleural ribs usually well developed.
21. Vertebrae commonly numbering 24, with usually equal numbers of caudal and precaudal elements, except in some elongate and in most fresh-water forms.
22. Hypural bones virtually always emanating from a single centrum; when on two centra, the hypurals no fewer than six in number, in no case formed as two hypural plates as in the *Paracanthopterygii*.
23. Caudal branched rays in most species 15, 17 in more primitive members of the group.
24. Fin spines present in most species.
25. Ctenoid scales common.
26. Presumably uniformly physoclistic.
27. Otophysic connections rare, in no case involving the intercalation of bony elements.
28. Viviparity uncommon.
29. Egg shape and buoyancy highly variable.

RELATIONSHIPS AND COMPOSITION OF CERTAIN SUPERORDERS, ORDERS, AND SUBORDERS

DIVISION I

SUPERORDER ELOPOMORPHA

The Elopomorpha are an assemblage of extremely diverse types varying from a group of primitive fishes sometimes classified with the holostean fishes (the Elopiformes; see Nybelin, 1957) to one group (the Saccopharyngoidei) showing such considerable modification of the syncranial architecture that it has been considered distantly related to all other bony fishes (Tchernavin, 1947a, 1947b).

It is difficult to discern over-all unifying characters among the Elopomorpha, but certain common intergroup characteristics can be recognized. For example, the ethmoidal commissure in the mesethmoid of Elopiformes and Notacanthiformes (in both instances associated with canal-bearing rostral ossicles) and the several resemblances (but especially the swim-bladder bauplan) between the Anguilloidei and the Notacanthiformes (see Marshall, 1962). The Saccopharyngoidei and Anguilloidei are linked through the nemichthyid-like eels. The sole

character found in every group is the possession of a leptocephalous larva. Larval stages are, of course, not known for every genus here included in the Elopomorpha, but leptocephalous larvae are known for every order and suborder.

Traditionally, the Elopiformes are linked with the clupeoid fishes (Regan, 1909; Berg, 1940), but in our opinion the relationship, if it exists, is very distant and probably is at the pholidophoroid level. The elopomorphs and clupeomorphs differ in many syncranial characters, of which particular reference may be made to the absence of a recessus lateralis in the elopomorphs (see p. 358), the presence in that order of roofed posttemporal fossae, of subtemporal fossae, a primary bite essentially of the tongue-parasphenoidal type, and of parietals that meet medially. The elopomorphs have a bone-enclosed ethmoidal commissure which is associated laterally with small, canal-bearing, rostral ossicles (Gosline, 1961). In *Albula* and *Pterothrissus* there is an extension of the infraorbital lateral-line canal onto the premaxilla. This character is probably unique among the living teleoste-

ans. Certainly no bone-enclosed ethmoidal canal is detectable in any clupeomorph fish, hence reinforcing the division between the elopiform and the clupeomorph fishes (see also Gosline, 1961, p. 35). Wohlfahrt (1937) described an ethmoidal commissure in *Sardina pilchardus*, but the canal is entirely superficial and not associated with an ossification.

The caudal skeleton differs considerably in the two groups (Hollister, 1936; Gosline, 1960; and this paper, pp. 358-359), except for the primitive clupeomorph *Denticeps* which approaches the condition of the elopiforms. *Denticeps* and the elopiforms possess the most primitive caudal fin skeletons known in living teleosts.

The characteristic otophysic connection of the clupeomorphs is described on page 358, where a comparison is also made with the only elopiform fish (*Megalops*) possessing an ear-swim-bladder linkage. In *Megalops* the cranial swim-bladder diverticula are lodged within bullae formed principally from the intercalars of each side (Ridewood, 1904; de Beaufort, 1909). This contrasts with the typical clupeomorph condition in which there are paired diverticula on each side, which are lodged in bullae of the prootics and pterotics.

Fairly marked differences in syncranial architecture occur between *Elops* and *Megalops*, on the one hand, and *Albula* and *Pterothrissus*, on the other (see Ridewood, 1904a). *Albula* and *Pterothrissus* present a somewhat more specialized picture, with the maxilla virtually excluded from the gape, the gular plate (a substantial bone in *Elops* and *Megalops*) greatly reduced and poorly ossified, and the parasphenoidal dentition absent from *Pterothrissus*. The elopiform lineage is an ancient one. Fossil elopiforms are found in Upper Cretaceous deposits of Europe, Africa, and Asia; the *Elops-Albula* dichotomy was established by at least Eocene times and probably earlier, since the genus *Istieus* (Upper Cretaceous) shows strong affinity with *Pterothrissus*.

The sum of morphological characters presented by the Elopiformes is, despite certain specializations of the Albuloidei, one of primitiveness. Yet it is difficult to derive from it any of the structural grades characterizing

the "primitive" members of other orders or superorders, particularly those of Divisions II and III. In other words, we believe that, once the elopiform level of organization was reached, the group entered an evolutionary *cul de sac*.

Two probable derivatives of the early elopomorph stem are the eels (Anguilloidei) and the Notacanthiformes.

The notacanth shares few characters with the other elopomorphs except in the possession of a well-developed and ossified ethmoidal commissure which is basically similar to that of the Elopiformes but differs from the peculiar ethmoidal chamber of the Anguilloidei (Allis, 1903; Gosline, 1961). The greatest resemblance in ethmoidal commissure arrangement is between the Albuloidei and the Halosauridae; in both the canal is hypertrophied and its bony walls are formed into an elaborate trellis. In body form and in most syncranial characters the Notacanthiformes differ considerably from the Elopiformes. Basically, the notacanth jaws are of a primitive type, with distinct premaxillae and maxillae forming the border of the upper jaw. No crossed ligaments are developed in relation to the upper jaw. However, the mobile palatoquadrate arch and the relatively immobile hyoid arch of the notacanthiforms are distinct specializations. Again, the loss of parasphenoidal teeth and of several elements in the neurocranium (autopalatines, supraorbitals, basisphenoid, orbitosphenoids, and pleurosphenoids) are specializations. The pectoral arch, although attached to the skull by a small or ligamentous posttemporal, has lost the mesocoracoids and postcleithra which are present in elopiforms (but absent from the Anguilloidei). The body of notacanthiforms is decidedly anguilliform, and the caudal fin skeleton is greatly reduced or absent.

As in the Elopiformes, the opercular apparatus of the Notacanthiformes is complete; it is considerably modified in the halosaurs (see Marshall, 1962, for a full discussion of this important taxonomic point) in which the preoperculum is greatly expanded. In that paper, Marshall also discussed in detail the nature of the fins in the three families here united as the Notacanthiformes. From a general consideration of their cranial anatomy (especially the opercular region), fin structure,

and swim-bladder anatomy, Marshall (1962) concluded that there are no grounds for maintaining two orders (Halosauriformes and Notacanthiformes) as proposed by Berg (1940).

The Notacanthiformes are an ancient group, at least as old as the Elopiformes. Fossil Halosauridae (*Echidnocephalus*, *Enchelus*) very similar to the extant *Halosaurus* occur in Upper Cretaceous deposits (Marck, 1858, 1863; Woodward, 1901). Similarities between these fossils and the extant *Halosaurus* indicate that little morphological change has occurred since the Upper Cretaceous. No fossil Notacanthidae are known. The fossil *Protonotacanthus* (Upper Cretaceous) is not a notacanthid and should perhaps be referred to the Protacanthopterygii (Arambourg, 1954). Likewise, the Cretaceous Dercetidae, thought by Boulenger (1904) to be notacanthid fishes, were shown by Arambourg (*ibid.*) to have myctophoid affinities.

Similarities between the Anguilloidei (Anguilliformes) and the Notacanthiformes, apart from the leptocephalous larva,¹ center principally on a fundamentally similar and otherwise unique bauplan for swim-bladder structure and organization (Marshall, 1962). Marshall is of the opinion that "... the resemblances are detailed enough to suggest that the Heteromi and Apodes evolved from a common ancestor, which must have been an isospondylous kind of teleost." He also considered a number of other similarities, including the absence of oviducts, the long, many-rayed anal fin, the abdominally situated, eight- to 10-rayed pelvic fins (comparing these with the eight-rayed pelvis of the fossil eel *Anguillavus*), the medioparietal skull, and the development of "spectacles" (a clear patch of head skin) over the eyes. Many of these characters require further study before convergence can be overruled (for example, the oviducts are absent from some members of the Salmoniformes, and the eel-like perciforms of the family Mastacembelidae have "spectacles" and a long anal fin). The anguillid-notacanth similarity in body form (especially the extreme modification of the caudal

fin) poses a particularly intriguing problem. Convergence seems less likely in this instance because of the markedly different ways of life characterizing the two groups. Gosline's views (1959) on factors molding the body form and skull structure of the Anguilloidei, i.e., their burrowing and hole-haunting habits, are particularly relevant in this connection as is the fact that several eels are bathypelagic but still retain the "typical eel" imprint. (Resemblances in body form between the Anguilloidei and Saccopharyngoidei seem to fall into the same category.)

The Anguilloidei differ from the Elopiformes and Notacanthiformes in many ways. The jaw structure is particularly divergent (the premaxilla fused with the ethmoid, upper jaw bordered both by the maxilla and the ethmopremaxillary bloc), and in eels there is a marked reduction in the size of the opercular elements. The reduction apparently is correlated with an increase in the importance of the branchiostegal rays as the supporting skeleton for the opercular membrane. (In *Cyema*, there are no branchiostegal rays and, apparently, no opercular elements.) As Gosline (1959) has shown, this modification of the gill covers is correlated with a peculiar pumping mechanism for the branchial current. To be effective, such a pumping device demands that the mouth and gill chambers be widely separated. The posterior displacement of the gills in eels has also resulted in the posterior displacement of the pectoral girdle, which thereby loses its connection with the skull.

As in the elopiforms and notacanthiforms, the parietals of the anguilloids meet medially (and may even fuse). A supraoccipital is usually developed, but it is wanting in the Serivomeridae, Nemichthyidae, and Cyemidae. In general the neurocranium is well ossified and forms a compact wedge (the families noted above being exceptions). The hyopalatine arch shows reductional trends, in no case consisting of more than three elements—hyomandibular, quadrate, and palatopterygoid. The last is often reduced to a thin lamina and is not infrequently absent. The hyomandibular and quadrate have an intimate, interlocking union; a symplectic does not develop.

Allis (1903) has described a peculiar me-

¹ We are indebted to Mr. Harrison for information, in press, about the halosaur leptocephalus he has recently discovered. A second halosaurid leptocephalus has been described by Mead (1965).

dian sensory chamber in the ethmoid of certain eels. Since the chamber is not linked with the supraorbital lateral-line canal, its homology with a true ethmoidal commissure is uncertain. However, the resemblance between the chamber and the ethmoidal canal of *Albula* (also without supraorbital connections) may be noted. Perhaps the anguilloid ethmoidal chamber should be considered in the light of the rather profound modifications that have taken place in the evolution of the anterior region of the skull in these fishes.

From the characters discussed above, it will be obvious that there are some, and apparently fundamental, resemblances among the Elopiformes, Notacanthiformes, and anguilloid Anguilliformes. On the other hand, these groups have diverged greatly in other characters. Since undoubted, if primitive, Anguilloidei also occur in the Cretaceous (*Urenchelys* [Woodward, 1901] and *Anguillavus* [Hay, 1903]) this divergence is of long standing.

Extreme specialization of the jaws, anterior vertebrae, and neurocranium make it difficult to assess the relationships of the Saccopharyngoidei. In most classifications (see Bertin and Arambourg, 1958) these bathypelagic fishes are included with or placed near the eels. Regan (1912b), however, believed them to constitute an order (Lyomeri) structurally quite unlike the eels, an order that ". . . may well have been derived from Iniomi such as the Synodontidae." This conclusion stands in sharp contrast to Regan's earlier views (1909) in which he allied the eels and saccopharyngoids. The most extreme view is that of Tchernavin (1947b), who believed that these fishes were distantly related to all other bony fishes. In our opinion, the relationship of the saccopharyngoids is with the Anguilloidei. Besides the presence of a leptocephalous larva several other characters suggest an anguilloid ancestry. Among these may be mentioned the great reduction or loss of the palatopterygoid arch (but see below); union of the hyomandibular and quadrate (no symplectic); loss of opercular elements (at least in the adult; see Orton, 1963); absence of ventral hyoid and branchial elements, at least in adults (a condition comparable with that of adult *Cyema*

[see Trewavas, 1933] but one that requires further research on adults and larvae of both groups); loss of branchiostegal rays (cf. *Cyema*); the marked anterior extension of the pterotics; and the development of mm. abductores mandibulae as the principal muscles for opening the mouth (again, cf. *Cyema* [Trewavas, 1933]). The Anguilloidei and Saccopharyngoidei are also similar in having the branchial skeleton displaced posteriorly and the pectoral arch free from the skull (mesocoracoid absent in both). In structural detail the branchial apparatus of the two groups is very different (Tchernavin, 1947a, 1947b), and the posterior displacement of the gills and girdle in the Saccopharyngoidei is probably attributable to the extreme development of the pharynx and not, as in the case of the eels, primarily to the displacement of the branchial apparatus.

The saccopharyngoids have a peculiar arrangement of the cephalic lateral-line system (the mandibular branch is absent), and the lateral-line organs are carried on papillae similar to those found in the Cyemidae among the true eels (a condition that occurs also in the ceratioid anglerfishes; see Trewavas, 1933).

Jaw structure in the eels and saccopharyngoids is very different. Indeed, the homology of the upper jaw bones in the Saccopharyngoidei is still doubtful. In adults, as Tchernavin (1947a) has shown, the upper jaw has the morphological relationships of a pterygoid arch. But, in the larva (Orton, 1963), there is an upper jaw which is morphologically normal, that is, in the maxillary position.

The Eurypharyngidae are unique among living teleosts in having five holobranchs and six visceral clefts.

Whereas differences between the Saccopharyngoidei and the Anguilloidei are several and marked, nothing in these differences suggests a relationship with other groups. With the exception of certain vertebral characters, the supposed resemblances between the Saccopharyngoidei and the Synodontidae (Myctophoidei), which Regan (1912b) listed, could be attributed to convergence correlated with the backwardly directed, upper-jaw suspension that occurs in both groups. The resemblances between

the saccopharyngoids and anguilloids are less likely to be the result of convergence. Within the Anguilloidei, many saccopharyngoid characteristics are present in the Cyemidae and Nemichthyidae.

The Monognathidae are an as yet imperfectly known group (Bertin and Arambourg, 1958), but one that nonetheless exhibits several characteristics of the Saccopharyngoidei. The larva is, however, unknown. Bertin and Arambourg (*op. cit.*) placed the family in a distinct order related to the saccopharyngoids, but the many resemblances to the latter do not seem to warrant such a division.

There is no fossil record for the Saccopharyngoidei.

SUPERORDER CLUPEOMORPHA

Despite the varied habitus of fishes included in this superorder, the Clupeomorpha are one of the most clearly defined aggregates of living teleosts. Three character complexes serve sharply to distinguish these fishes, viz., the type of ear-swim-bladder connection, the architecture of the neurocranium (especially the relationship of certain lateral-line canals to one another and to the ear), and the supporting skeleton of the caudal fin.

In all living clupeomorphs there is an intimate intracranial connection between the swim bladder and the inner ear. With very few exceptions the swim-bladder diverticulum of each side divides within the skull to form two large vesicles which are lodged within ossified bullae of the prootic and pterotic bones. The connection between these vesicles and the ear have been described in detail by Wohlfahrt (1936). In the exceptional genera (e.g., *Sprattus*), only the prootic vesicle is developed. This unity of swim-bladder bauplan in the Clupeidae, Chirocentridae, and Denticipitidae led Marshall (1962) to suggest that the families should be united in a distinct division of the suborder Clupeoidei.

The clupeomorph ear-swim-bladder connection is unlike that occurring in any other group of fishes. In *Megalops*, for example, the single vesicle of each side is lodged within an intercalary vesicle, whereas in the Notopteroidae (see p. 362) the greater part of the vesicle is extracranial. In the notopterid

Papyrocranus, however, some intracranial invasion has taken place, but this invasion differs in detail from that found in the Clupeomorpha. In the Mormyriiformes the vesicles are intracranial but are situated in yet another part of the skull, are not encapsuled, and have lost their connection with the swim bladder in adults.

Three remarkably constant features in the skull of clupeomorphs are the temporal foramina (bordered by the frontals and parietals), the pre-epiotic fossae (bounded by the parietal, pterotic, and epiotic of each side), and the auditory fenestrae (surrounded by the prootics, exoccipitals, and basioccipitals). The relative sizes of these apertures show considerable interspecific variation, and from some genera one or, more rarely, two may be absent; in most cases all three openings are present. A fourth and invariable feature of the clupeomorph neurocranium is the recessus lateralis, a chamber developed on the medial aspect of the pterotic and separated from the perilymph cavity of the inner ear by a thin membrane. The supraorbital, infraorbital, preopercular, and pterotic lateral-line canals all open into this chamber. Perhaps concomitant with the development of the recessus is the fact that the openings of the infraorbital and preopercular canals into it are very close together; in some instances the openings are virtually confluent, being at most separated by a narrow bar of bone. Externally, the presence of this confluence is indicated in all clupeomorphs by the way in which the upper parts of the two canals approach each other. As far as we can determine, the recessus lateralis is a unique feature of the Clupeomorpha.

With the exception of the Denticipitoidei, the caudal fin skeleton is remarkably similar in all clupeomorphs and is of a type immediately recognizable by several diagnostic features (Gosline, 1960; Hollister, 1936). One of these features is the way in which the second hypural lacks a basal articulation with the "urostyle," from which it is separated by a distinct gap. There is always a certain degree of consolidation manifest in the caudal skeleton; the urostyle is formed by the fusion of the terminal vertebra and the first uro-neural. In some genera the caudal fin support is unicentral, but in others a distinct centrum

is preserved posterior to that which carries the first or lowermost hypural.

The Denticipitoidei have a caudal fin skeleton of an extremely primitive type. Three or possibly four centra are involved, the second hypural (together with the third) is articulated with a centrum, the first uroneural extends to the centrum of the first hypural but is not fused with it (apparently only one uroneural is present), and small neural arches are present on the two centra which carry the first three hypurals. In certain respects (especially the high number of discrete centra involved, and because the second hypural has not lost its basal articulation) the caudal skeleton of the denticipitoids resembles that of an early larval clupeid (see Hollister, 1936). However, in its general organization, it shows a degree of differentiation more comparable with that of a larval clupeid in a later stage of differentiation, that is, when the second hypural has lost its articulation with a centrum.

Other characters of widespread occurrence in the Clupeomorpha as a whole are: the virtual absence of lateral-line pores on the trunk (except in the Denticipitoidei in which a complete line is developed), the presence of radiating cutaneous canals on the opercular bones (the canals open into the lateral-line system but are themselves without neuro-masts), absence of parasphenoid teeth, no posttemporal or subtemporal fossae, and the development of keeled scutes along the ventral midline of the abdomen.

The shape of the head and of the jaws among clupeomorph fishes is variable, although usually the mouth is terminal and moderately large and the dentary has a high coronoid process. Most clupeomorphs are microphagous, and there is a marked tendency toward a reduction in oral and buccal dentition, and a trend toward the development of suprabranchial organs associated with the fourth and fifth gill arches. An exception to this generalization is, of course, the predaceous *Chirocentrus*, which has large, fang-like teeth in the jaws. In no clupeomorph are the jaws protrusile. Ecologically, the superorder may be considered one of characteristically marine, pelagic, and shoaling fishes. There are, however, numerous fresh-water representatives, particularly in tropical Africa and India.

The Denticipitoidei are known only from a single extant and monotypic genus in certain west African fresh waters, and a very closely related fossil from east Africa (Clausen, 1959; Greenwood, 1960). Superficially these fishes have a very clupeoid appearance, but they are immediately distinguished from the Clupeoidei by the presence of denticles on all the roofing bones of the skull and even on some trunk scales. Anatomically the suborder is distinguished by the primitive caudal fin skeleton (see above) and by several characters in the syncranium (see Clausen, 1959; Greenwood, 1960, 1963, and 1965) of which may be noted the lateral-line system with its distinct frontal branch, the enlarged, gutter-like, and medially contiguous nasals, and the general morphology of the skull, particularly its smooth, almost larval, contours. Nevertheless, these peculiar little fishes have the clupeomorph characters of a recessus lateralis, prootic and pterotic bullae for the swim-bladder vesicles, a temporal foramen, and extensive lateral-line canals on the operculum. Considering, especially, the nature of the caudal fin skeleton, the morphology of the neurocranium, the structure of the jaws, and the presence of a complete trunk lateral line, we believe that *Denticiceps* is the most primitive living clupeomorph. The peculiar cephalic denticles and the absence of a supramaxilla are specializations, but these in no way obscure the generally primitive level of organization demonstrated in so many other characters.

Traditionally, the fishes here grouped in the Clupeomorpha are allied with *Elops*, *Megalops*, and *Albula*. Berg (1940), for instance, places all three genera in one suborder. On the basis of the three major characters discussed above (otophysic connections, neurocranial architecture, recessus lateralis), we think that the Clupeomorpha are not closely allied to the elopoids and albuloids. Yet another difference between the two groups is the occurrence in the elopoid-albuloid aggregate of a leptocephalous larva.

In most respects the albuloids and elopoids do not provide a suitable type of organization from which to derive the Clupeomorpha, especially the rather specialized clupeoids, nor is it possible to derive the Denticipitoidei from the elopomorphs or *vice versa*. But the

denticipitoid grade (apart from the loss of supramaxillae and the presence of cephalic denticles) could well be basic to that of the clupeoids. The fundamental question is, Can the proto-elopomorphs and proto-denticipitoids be derived from a common stem? At present the question cannot be answered. In essence an answer first requires the elucidation of how the clupeoid type of otophysic connection and the recessus lateralis were evolved. These two features, and perhaps also the characteristically clupeomorph cranial apertures, may be functionally interrelated. From evidence currently available from both living and fossil fishes of the elopomorph and clupeomorph types, there is even the suggestion that the two groups had a long separate history. Indeed, we have even given serious consideration to the possibility that the Clupeomorpha should be recognized as a distinct division of teleosts.

Although fishes known only from fossils are not under revision in this paper, some comment is needed on those extinct forms usually classified with the clupeoids.

Several extinct genera (e.g., *Ichthyodectes*, *Xiphactinus*, and *Thrissops*) are supposed to have some relationship with the Chirocentridae, a family showing several "primitive" characters. In our opinion, such belief is premature, and the fossil material should be reviewed with regard to clupeomorph characters described here. Thus we cannot agree with Saint-Seine's (1949) or Bardack's (1964) placement of these and other genera in the Chirocentridae. Indeed, our own observations, coupled with the characters listed by Bardack (*ibid.*), suggest that members of his *Spathodactylus-Xiphactinus* line (including the genera *Ichthyodectes* and *Xiphactinus* [= *Portheus*] which we have studied) show certain affinities with the Osteoglossomorpha. Of particular significance in this connection are the basipterygoid process, the dentition, the presence of a subtemporal fossa like that in *Osteoglossum*, and the medially united parietals. We suggest that these fishes may represent an early offshoot from the osteoglossid line; at present we are uncertain about the placement of those extinct genera which Bardack (*ibid.*) put in his *Thrissops-Chirocentrus* line. Our detailed examination of a *Thrissops* species, together with informa-

tion gathered from the literature, certainly suggests that this genus, and *Pachythrissops* (*sensu* Nybelin, 1964), differ from the clupeomorphs in many ways.

The Clupavidae are an extinct family (Lower to Middle Cretaceous) of particular interest. Currently, the clupavids are accepted as clupeoids having some affinity with the round-herrings (Dussumierinae). Recently, Whitehead (1963) has challenged this supposed relationship and has suggested that the clupavids may be "... between the elopoids and Chirocentridae." Judging from Arambourg's reconstruction and figured material (Arambourg, 1954), we find difficulty in accepting either interpretation and suggest a third. The caudal fin skeleton of the Clupavidae is, in many respects, clupeoid. That is, a distinct "urostyle" is developed, and the major hypurals (excluding the first) articulate with it. But the second hypural is included and not free basally as it is in all living clupeoids. The relationship of the infraorbital and preopercular lateral-line canals in the Clupavidae differs from that of all living clupeomorphs: they do not approach each other proximally and have widely separated openings into the supraorbital canal. This canal arrangement suggests that no recessus lateralis was developed in these fishes. Also, none of the typical clupeomorph cranial openings has been described in the Clupavidae. Thus, in these characters the clupavids cannot be considered as like the Clupeomorpha, despite their resemblance to this group in their general facies and, especially, in their jaw morphology. Regrettably, no data are available on the endocranial morphology of the Clupavidae, so we cannot tell whether or not prootic and pterotic bullae are present.

In many respects, the Clupavidae resemble the Leptolepididae, a family of uncertain position (sometimes considered holostean) and known from deposits of Middle Triassic to Upper Jurassic age (see also Rayner, 1936). There is nothing in the structure of the leptolepidids that could militate against their being ancestral to the Clupavidae. We therefore suggest that a leptolepidid-clupavid phyletic line was independently derived from the pholidophoroid stem and represents a convergent evolutionary trend toward that of the clupeomorphs. If any common ancestry

for the two lines is sought, it should be looked for among the pholidophoroid holosteans.

DIVISION II

SUPERORDER OSTEOGLOSSOMORPHA

The extant Osteoglossomorpha are freshwater fishes confined, with one exception, to the tropical regions of South America, Africa, southeast Asia, New Guinea, and Australia. The exceptional genus, *Hiodon*, occurs in North America. Undisputed osteoglossomorphs occur as fossils in fresh-water Eocene deposits of Sumatra, Australia, and North America; the supposed Osteoglossidae from the Eocene of Europe and North Africa require, in our opinion, further study before their affinities can be determined.

Despite the considerable range of body form and jaw structure in members of this superorder, the group is readily distinguished by two characters common to all members, and by a number of other characteristics with a mosaic pattern of distribution among its members.

All Osteoglossomorpha have the primary bite between the parasphenoid and the tongue (basihyals and glossohyal), the bones involved being well toothed. In one genus only, the osteoglossid *Clupisudis* (= *Heterotis*), is the primacy of the parasphenoid-tongue bite reduced by the absence of teeth on the parasphenoid and by a great reduction in the toothed area of the tongue. This loss apparently is a secondary one because *Clupisudis* shows many of the other characters associated with the typical condition. That *Clupisudis* is the only microphagous osteoglossomorph (the others are all predaceous) is undoubtedly significant, as is the development in this genus alone among the osteoglossomorphs of suprabranchial helices associated with the fourth and fifth gill arches (d'Aubenton, 1955). Probably associated with a primary parasphenoid-tongue bite is the fact that the maxillae show a greatly simplified association with the palatines. There is no process for articulation between the maxilla and palatine, the latter ending anteriorly in a simple point. When bony articulations are developed between the skull and the palatopterygoid they are either between the

parasphenoid and the entopterygoid (Osteoglossoidi) or through fusion of the palatines with the vomer (Mormyriiformes). In most Osteoglossomorpha, the maxillae are well toothed, they form the greater part of the upper jaw, and they are aligned in overlapping tandem with the premaxillae. The maxilla and premaxilla are firmly bound together and have restricted mobility; only in the Mormyriiformes are the maxillae edentulous, relatively motile, and partially excluded from the gape. In that order, the maxillae are articulated with the ethmoid, behind and above the premaxillae. Supramaxillae are wanting in all osteoglossomorphs. The premaxillae are firmly bound to the skull and have apparently very restricted motility. In Mormyriiformes and in *Pantodon*, alone of the Osteoglossiformes, the premaxillae are fused; they are closely apposed medially in Notopteroidei and in most Osteoglossoidi.

The second "group character" is the development of paired, usually ossified, rods at the base of the second gill arch in all Osteoglossomorpha. These tendon bones develop in association with the second hypobranchial (Osteoglossoidi and Mormyriiformes) or the second basibranchial (Notopteroidei; they are uncalcified in *Hiodon*).

The hypobranchial skeleton is variously developed in the superorder (see Ridewood, 1904b, 1905a). Unossified first basibranchials are a feature of *Pantodon* and *Clupisudis* (Osteoglossoidi) and in the Notopteridae among the Notopteroidei.

Characters of general occurrence, besides the presence of paired subbranchial tendon bones, and the parasphenoid-tongue primary bite, are the fused parapophyses and the absence of lower intermuscular bones. The epineurals are confined to a few anterior vertebrae in many cases.

The caudal fin skeleton is of particular interest. In two families, the Notopteridae (Osteoglossiformes) and the Gymnarchidae (Mormyriiformes), it is greatly reduced and there is no distinct caudal fin. All other members of the Osteoglossomorpha have a distinct caudal fin, and in all except the Hiodontidae (Notopteroidei) there is a great similarity in its supporting skeleton. An outstanding characteristic is the considerable degree of consolidation among the upper hypurals

which are also fused with the uroneurals and apparently with a vertebral centrum (Gosline, 1960 and 1961). Attempts to determine the homologies of these elements raise several difficulties, but, whatever solution is accepted, the caudal fin skeleton of the Osteoglossomorpha is quite distinctive and unlike that of any other teleost (see Gosline, 1960). The trend toward fusion shown by the Osteoglossoidei and all Mormyriiformes with distinct caudal fins is carried to extremes in the Notopteroidei and in the Gymnarchidae (Mormyriiformes) which do not have an externally distinct caudal fin. By contrast, the Hiodontidae (Notopteroidei) have an extremely primitive caudal skeleton, with a full complement of hypurals and uroneurals supported on three centra, the two anterior of which retain neural arches and spines. All osteoglossomorphs with a distinct caudal fin have 19 or fewer principal fin rays; one (*Osteoglossum*) has only 10.

The pelvic fins are abdominal in all genera except *Pantodon*, in which they are thoracic; however, there is no connection between the pelvic and pectoral girdles.

All members of the Osteoglossiformes, except *Pantodon*, have characteristically ornamented scales in which the radii form a coarse and irregularly reticulated pattern, both apically and basally; no reticulum is developed in the scales of *Pantodon*. A similar reticulum occurs in the scales of the Mormyriiformes, but it is confined to the apical area. Cockerell (1910a, 1910b) noted that in Mormyriiformes the circulae are moniliform, but in the Osteoglossidae they are continuous. However, in the Eocene fossil osteoglossid *Phareodus* an intermediate condition is found. The scales of the Notopteroidei do not resemble either the osteoglossid or the mormyriiform types.

Characters of the syncranium have a mosaic distribution within the superorder.

Most osteoglossomorphs have an orbitosphenoid (*Osteoglossum* and *Scleropages* of the Osteoglossidae are exceptional); a basisphenoid is present in some (Notopteroidei and certain Mormyriiformes); posttemporal fossae occur only in the Osteoglossidae (except in *Pantodon*) as do subtemporal fossae (the fossa being more of a groove in *Clupisudis* and *Pantodon*). An extrascapular is present in all groups; it is a small bone in the Osteo-

glossoidei and some Notopteroidei (*Notopterus* and *Xenomystus*) but is an extensive, shieldlike bone in other notopteroidei (*Papyrocranus* and, especially, *Hiodon*) and in all Mormyriiformes. The parasphenoid is generally toothed but is edentulous in *Clupisudis* among the Osteoglossoidei and in some mormyriiform species.

Apart from the Osteoglossoidei, all members of the Osteoglossomorpha have, at some stage in ontogeny or throughout life, a connection between the otic region and the swim bladder effected through a pair of forwardly directed diverticula of the swim bladder. In the Notopteroidei, the connection persists throughout life, the swim-bladder diverticula being closely applied to the lateral aspects of the otic region; an auditory fenestra is developed (see Greenwood, 1963; Dehadrai, 1957). In one genus (*Papyrocranus*) extensive intracranial swim-bladder diverticula are also present (Greenwood, 1963). In Mormyriiformes the otophysic connection is broken during ontogeny, but two vesicles remain lodged in each lateral cranial foramen or fossa (in Gymnarchidae). This fossa is an aperture bordered by the pterotic, epiotic, and exoccipital, and is roofed by the extrascapular. The lateral cranial foramen or its homologue (Greenwood, 1963) is present in the Notopteroidei and in the Mormyriiformes, but no such aperture is present in the Osteoglossoidei, thus suggesting an early dichotomy in the basic osteoglossomorph stem associated with the evolution of an otophysic connection. In no species is the otophysic connection like that found in the Clupeomorpha (see p. 358), in which distinct intracranial osseous bullae are developed in association with the inner ear. Nor is the connection like that of *Megalops* (Elopomorpha), in which the swim-bladder diverticulum of each side is lodged in bullae formed from the intercalar laterally and the prootic, exoccipital, and basioccipital medially.

The inner wall of the swim bladder is partly alveolate in *Arapaima* and *Clupisudis* (Osteoglossidae), completely so in Pantodontidae (Nysten, 1962), smooth in other members of the Osteoglossidae and in all Mormyriiformes except the Gymnarchidae in which it is alveolate. The abdominal portion of the swim bladder in the Notopteroidei is

completely subdivided (Dehadrai, 1957; Greenwood, 1963) but is simple and tubular, with smooth walls, in the Hiodontidae. In the Notopteridae, there is a considerable postabdominal extension of the swim bladder formed by paired diverticula lying on each side of the vertebral column; ventrally each diverticulum is produced into a number of viliform caeca. The notopterid condition is also seen in *Osteoglossum*, whereas in *Clupeisudis* there is a short postabdominal extension contained within the haemal arches. In all other Osteoglossomorpha there is no postabdominal extension.

Throughout the Osteoglossomorpha there is a tendency for certain elements of the palatopterygoid arch to fuse. In the Osteoglossoidei the ectopterygoid and palatine are fused, as they are in the Notopteroidei, although in *Hiodon* these elements are separate but firmly joined. In the Mormyriiformes the ectopterygoid, entopterygoid, and palatine are fused, and the latter is also fused with the vomer. Ectopterygoid, entopterygoid, and palatine teeth are of common occurrence, although in some members of all groups certain or all of these bones may be toothless. All, for example, are toothless in the Mormyriiformes.

The Osteoglossoidei alone are characterized by an articulation between a ventrolaterally directed peg of the parasphenoid and the entopterygoid. No other group of extant teleosts has such a joint.

A typically mosaic reductional trend is seen in the opercular series. In *Hiodon* (Notopteroidei), all Osteoglossoidei (except *Pantodon*), and the Mormyriiformes, a small to very small suboperculum is present, but this bone is wanting in *Pantodon* and in the other members of the Notopteroidei.

Circumorbital bones are best developed in the Osteoglossiformes (the extensive postocular bones completely cover the cheek) but show some reduction in the Notopteroidei (especially in the postocular series of the Notopteridae; those of the Hiodontidae being somewhat more extensive). Greatest reduction is found in the Mormyriiformes, in which the whole series is affected but often differentially. The Notopteridae exhibit a most peculiar development, namely, an extensive subocular shelf formed from the sec-

ond and third suborbital bones. A subocular shelf is elsewhere found only in certain living and extinct Acanthopterygii.

A number of unique and interrelated characters are found in the Mormyriiformes, for example, the caudally situated electric organs (modified body muscles), the very large cerebellum, and peculiarly modified neuromasts (so-called mormyromasts); the epidermis has a peculiar histological structure (Franz, 1920). Above and below each electric organ there is a thin, tendinous bone (bones of Gemminger) of unknown function.

Ridewood (1905a) gave a summary of the early taxonomic history of the Osteoglossidae. From his account it is clear that several authors tended to associate this family with the Hiodontidae, Notopteridae, and Mormyridae. Dissenting opinions were those of Woodward and Boulenger who related the osteoglossids to the Albulidae, a view endorsed by Ridewood himself (1905a), but one that is difficult to substantiate when the characters discussed above are taken into account. Ridewood (1904b) also summarized the history of the Mormyridae, Notopteridae, and Hiodontidae. On the basis of his craniological studies Ridewood concluded that "... the families Mormyridae, Notopteridae and Hiodontidae, though more closely related *inter se* than is either family with any other family of Malacopterygian fishes are not more intimately related with one another than was previously assumed to be the case." Regan (1909) associated the three suborders Osteoglossoidei, Notopteroidei (including the Hiodontidae), and Mormyroidei within his order Isospondyli, but he did not propose any formal grouping of the three.

Garstang's (1931) rather revolutionary classification places the families considered here in two divisions (Hyodontoidae and Mormyroidei) of a larger group, the Osteoglossi, in which he also placed the Elopoidei and Clupeoidei. The Osteoglossi are coordinate with the Plectospondyli (=Ostariophysii) in Garstang's section Otophysi of the Malacopteri. The Otophysi were defined on the basis of the members' having, usually, swim-bladder-otic connections. In view of the very different otophysic connections of the Ostariophysii, the Clupeidae, Hiodontidae, and Notopteridae, and *Megalops* among the

Elopidae, it is impossible to accept Garstang's Otophysi as a phyletic assemblage. Moreover, there are no substantial reasons for including the elopoid and clupeoid fishes in a division with the osteoglossiforms and mormyriiforms. Garstang relied almost entirely on the presence of ". . . opposing teeth on hyoid and parasphenoid." This character is developed in some elopoids but is hardly a characteristic of the clupeoids, and there are many differences between the elopoids and osteoglossoids which militate against close relationship.

Gregory (1933) also proposed a formal grouping by uniting the Notopteridae, Hiodontidae, and Mormyridae (including *Gymnarchus*) as a superfamily (Mormyroidea) of the Isospondyli. In Gregory's scheme the Mormyroidea are immediately preceded by the Osteoglossoidae (comprising the Osteoglossidae and Pantodontidae); his only comments on a possible relationship between the two superfamilies were confined to a remark on similarities between the pectoral girdles and certain aspects of syncranial architecture in *Hiodon* and *Osteoglossum*. Gregory (1933) also gave a good historical summary of views on the relationship of the Osteoglossoidae and Mormyroidea.

Gosline (1960) suggested a formal grouping of the hiodontids, notopterids, and osteoglossids. He united them in a suborder (Osteoglossoidae) which forms a distinct division (Osteoglossi) within the Clupeiformes, all other isospondyls being placed in the division Clupei. Gosline did not give a detailed account of relationships between the Osteoglossi and the Mormyriiformes, but he acknowledged the existence of some relationship (1960, 1961). Greenwood (1963) elevated Gosline's division Osteoglossi to ordinal status (Osteoglossiformes) and commented on the relative isolation of the order from other living Isospondyli. Greenwood, like Gosline, acknowledged the probable interrelationship of the Osteoglossiformes and Mormyriiformes. The latter they thought to be derived from some branch of the notopterid-hiodontid line, but details were not given.

No fossil Mormyriiformes are known and the only fossil Notopteridae are from Lower Tertiary beds (?Eocene) of Sumatra, the fish being identified as *Notopterus notopterus*, a

species still living in India (Sanders, 1934). The record for the Osteoglossidae is somewhat better. An extinct genus, *Phareodus*, occurs in Eocene fresh-water deposits of Wyoming, Tertiary beds in Queensland (Hills, 1934), and in Tertiary (?Eocene) deposits of Sumatra (Sanders, 1934). From the Sumatran beds, Sanders also identified some typically osteoglossid scales as those of *Scleropages*, a genus still surviving in the Indo-Australian Region. The genus *Brychaetus*, known from fossils of Eocene age in Europe and North Africa, is usually included in the Osteoglossidae. As yet, the osteology of *Brychaetus* does not seem sufficiently well known to warrant such action. However, the genus should probably be referred to the Osteoglossiformes, perhaps as a distinct suborder; *Brychaetus* may have been a marine species.

The extinct family Plethodontidae, represented by several genera from Upper Cretaceous deposits in Europe, North Africa, and North America and usually classified with the osteoglossoids, is, in our opinion, insufficiently known to warrant its inclusion in the Osteoglossomorpha.

The possible relationships of at least some members of the extinct and supposedly clupeoid family Ichthyodectidae (included in the Chirocentridae by Saint-Seine, 1949, and Bardack, 1964; see also Nybelin, 1961 and 1964) with the Osteoglossomorpha is discussed above.

Most Osteoglossidae are large to moderately large fishes with predaceous feeding habits. Exceptional are *Clupisudis*, which although conforming to the modal size is a microphagous species, and *Pantodon*, which conforms to the trophic mode (it is insectivorous) but is small, rarely exceeding a length of 10 cm. All osteoglossids are robust-bodied fishes with a large gape; the body is either somewhat compressed (*Osteoglossum* and *Scleropages*) or rounded to subrectangular in cross section, In *Pantodon* the pectoral fins are greatly enlarged, and the fish skitters along the water surface.

The Notopteroidei are also large-mouthed, predaceous fishes. The Notopteridae are elongate, laterally compressed fishes of moderate to small size; the Hiodontidae are less compressed and deeper bodied, with distinct caudal fins, and are of moderate size.

A greater range of mouth size and form is encountered among the Mormyriiformes. Generally, the mouth is small, although some large-mouthed species are known. The head shape is extremely varied but with a trend toward elongation of the snout into a narrow, decurved tube. In general, the Mormyriiformes are somewhat compressed, dark-colored fishes of small to moderate size, and are insectivorous.

On all counts, the Osteoglossoidei represent a radiation distinct from that of the Notopteroidei and Mormyriiformes, and in most respects show a more primitive level of organization. The mormyriiform radiation is undoubtedly the most specialized, but in many anatomical points members of this order show clear indications of their derivation from a hiodontoid-notopteroide stock. On this latter line, the Hiodontidae are undoubtedly the most primitive members.

The geographical distribution of the Osteoglossomorpha is of considerable interest. The Osteoglossoidei occur in Africa (*Clupisudis* and *Pantodon*), South America (*Arapaima* and *Osteoglossum*), and the Indo-Australian Region (*Scleropages*). Most members of the Notopteroidei occur in India or Africa (Notopteridae: *Notopterus*, *Papyrocranus*, and *Xenomystus*), but the Hiodontidae (*Hiodon*) are confined to North America. The Mormyriiformes (Mormyridae: numerous genera; and Gymnarchidae: the monotypic genus *Gymnarchus*) are confined to Africa, particularly the tropical regions.

As mentioned above, Ridewood (1905a) suggested a relationship between the Osteoglossidae and the Albulidae. There are, admittedly, some points of similarity in the syncranial architecture of the two families, especially in the well-toothed parasphenoid, palatopterygoid arch, and the tongue, and in the presence of subtemporal and posttemporal fossae. There are, however, many more dissimilarities. For example, the two families differ in the jaw structure, the presence or absence of paired tendon bones, the nature of the caudal fin support, the ornamentation of the scales, and the presence or absence of a parasphenoid-entopterygoid articulation and of a leptocephalous stage in ontogeny. Not all the differences are clearly attributable to specialization in one family or the other. The

characters shared by the two families (except perhaps the intrabuccal dentition) can as well be considered basic teleostean characters as indicators of close phyletic relationships.

In another paper Ridewood (1904b) justified his rejection of Boulenger's (1898) views of an albulid-mormyrid relationship in a closely detailed argument (which we accept), but he did not propose any other possible relationship except to group them loosely with the notoapterids and hiodontids.

Our reasons for relating the families here associated as the Osteoglossomorpha are discussed above (pp. 361-363). On the basis of these characters we are unable to find any obvious relationships outside the association. Fossil evidence may show some connections, but for the moment we assume that the Osteoglossomorpha represent a distinct phyletic group within the teleostean level of organization.

Important works on the taxonomy and anatomy of the Osteoglossomorpha include the following. General works are: Berg (1940), Boulenger (1898), Cockerell (1910a, 1910b), Garstang (1931), Gosline (1960, 1961), Gregory (1933), and Regan (1909). Studies on the Osteoglossoidei are: d'Aubenton (1955; suprabranchial organ of *Clupisudis*), Daget and d'Aubenton (1957; skull of *Clupisudis*), Gosline (1960; caudal fin skeleton; taxonomy), Greenwood and Thomson (1960; pectoral girdle of *Pantodon*; taxonomy of Pantodontidae and Osteoglossidae), Nyssen (1962; swim bladder and visceral anatomy of *Pantodon*), and Ridewood (1905a; syncrania of the Osteoglossidae and Pantodontidae; taxonomy of these families). Studies on the Notopteroidei are: Dehadrai (1957; swim bladder in *Notopterus*), Gosline (1960; caudal skeleton of *Hiodon*; taxonomy), Greenwood (1963; swim bladder in the Notopteridae and Hiodontidae; skull in the Notopteridae; taxonomy), Omarkhan (1949b; sensory canals of *Notopterus*), Omarkhan (1950; chondrocranium of *Notopterus*), and Ridewood (1904b; syncrania of the Notopteridae and Hiodontidae; taxonomy). Studies on the Mormyriiformes are: Daget and d'Aubenton (1960; chondrocranium of *Mormyrus rume*), Gosline (1960; caudal fin skeleton), Omarkhan (1949a; chondrocranium of *Gymnarchus*), Ridewood (1904b; syncrania

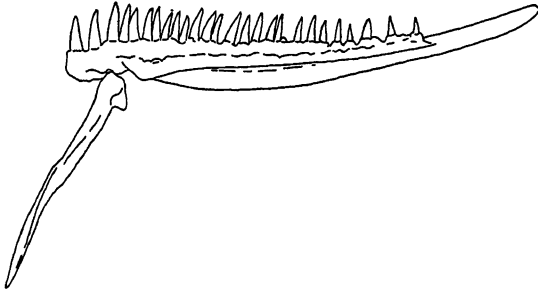


FIG. 2. Right upper jaw bones of *Dallia pectoralis* seen in front quartering view. Anterior up. Note that the toothed premaxilla extends in front of most of the length of the edentulous maxilla and that the lanceolate proethmoid is bound to the symphyseal edge of the premaxilla and projects backward (downward) in approximately the orientation of an ascending premaxillary process.

of the Mormyridae and Gymnarchidae), Stipetić (1939; auditory organs of the Mormyridae).

DIVISION III

SUPERORDER PROTACANTHOPTERYGII

Several reasons lie behind our establishment of the Salmoniformes as constituted below, and as the principal element of the Protacanthopterygii. First, we are unable to find a combination of anatomical characteristics that satisfactorily distinguishes the Myctophoidae (formerly the Myctophiformes, Scopeliformes, or Iniomi) from those fishes that are usually grouped as the Salmonoidei and Esocoidei. It is true, of course, that some myctophoids show various advanced features of the jaws, opercular apparatus, fins, and caudal skeleton, but there are a great many that do not. As a result, the group has in the past been distinguished from the salmonoids and their allies in the old Clupeiformes, *sensu lato*, chiefly on the superficial basis of the fact that the upper jaw is bordered by the premaxillae alone. Such a separation cannot be maintained, however, for this condition of the upper jaw is to be found also in galaxiids, aplochitonids, and umbrids (*Dallia*, see fig. 2), among others. If one reviews the structural details of the salmonoids, argentinoids, galaxioids, esocoids, and stomiatoids, it is evident that the main characteristics of the myctophoids are merely the "advanced" features of the first five groups collected to-

gether. In other words, some members of the group, including the Salmonoidei, Argentinoidae, Galaxioidei, Esocoidei, and Stomiatoidae, and some or all members of the Myctophoidae, exhibit the exclusion of the maxilla by the premaxilla from the gape, the consolidation of the hypural bones onto a terminal half-centrum, the loss of an orbitosphenoid and of a mesocoracoid, the acquisition of photophores, and the development of an adipose fin. Nevertheless, some myctophoids have progressed further in the direction of the Acanthopterygii than has any other salmoniform species. Examples of this progress are the elevated pectorals and advanced pelvics of the Aulopodidae, the acanthopterygian-like jaws and hyoid and branchiostegal apparatus of the Neoscopelidae (fig. 3), and the berycoid-like principal caudal fin-ray formula of numerous families, including the Synodontidae and Myctophidae. Hence, the ancestors of the living myctophoids may justifiably be suspected of having also contributed to the ancestry of certain major percomorph types.

This general view of percomorph ancestry may be further explored by a more detailed consideration of the probable origin of the very advanced condition of the upper jaw of *Neoscopelus*, a condition that is closely approached by the jaws of myctophids and galaxiids. In *Neoscopelus* the premaxilla, which entirely excludes the maxilla from the gape of the open mouth, has two processes, one at its proximal or symphyseal end, and the other on the shaft of the bone near its distal end. The symphyseal process is subtriangular and ventrally concave, forming a canopy over a complex maxillary process. The symphyseal premaxillary process and the underlying maxillary process which articulates with it have a ligament that contributes to the support of the upper jaw. The maxillary ligament extends obliquely backward and toward the midline where it is seated on one side of the mesethmoid bone; the maxillary ligament is crossed by the premaxillary ligament that extends between the premaxillary process and the head of the palatine. The distal premaxillary process is a thin shelf of bone on the posterodorsal margin of the shaft, and on which the maxillary shaft rests when the mouth is nearly or completely closed. Similar processes

have been found in myctophids and galaxiids, but their symphyseal elements are not associated with a set of crossed rostral ligaments.

There is general agreement that the distal premaxillary process that rests against the shaft of the maxilla is the same element in all fishes. The homologies of the symphyseal or proximal premaxillary processes (the articular and ascending) are equivocal, however, and there has been no general agreement on their origin, function, terminology, or occurrence in fishes. The first major effort to understand the origin of the articular and ascending processes, hence to determine their homologies in various groups of fishes, was made by Allis (1909). He wrote: "[The articular and ascending] . . . processes of the premaxillary both arise from the proximal end of the bone, and, in the description of many fishes, are both included under the term ascending process. But one of them only is properly that process, the other being a greatly developed articular process. [The proper ascending process is a] . . . long, thin, pointed, plate-like piece of bone which lies in a plane that crosses obliquely and perpendicularly the extreme proximal end of the premaxillary. Its internal surface is presented ventro-postero-laterally and its mesial and larger part rests upon and is firmly attached by connective tissue to the corresponding half of the grooved dorsal surface of the cartilaginous rostral, its mesial edge touching, throughout nearly its entire length, in the mid-dorsal line, the corresponding edge of its fellow of the opposite side."

Allis also concluded that a proper ascending process must have a ligament to the palatine crossing an ethmomaxillary ligament. If so, then neoscopelids, as well as cods and their relatives, have the ascending process much reduced and consolidated with the adjacent articular process, for in these forms the palato-premaxillary ligament is present, but a distinct ascending process often is not. Allis further distinguished the ascending process from the articular process as follows: "The articular process of the premaxillary arises from the bone immediately lateral (distal) to the ascending process. It is a relatively large plate of bone which lies in a plane that begins at the antero-lateral edge of the base of the

ascending process, at an acute angle to the plane of that process, and from there runs postero-laterally across the dorsal surface of the body of the bone."

In an earlier paper, Allis (1898) had concluded that the ascending process of the premaxilla of teleosts is primarily an independent bone, represented in the median dermal ethmoid of *Amia* and in the proethmoid of *Esox*. With this conclusion we concur, on the basis of the close functional association between the head of the premaxilla and the dermal ethmoid. Our preparations of the skull of *Dallia* indicate that during heavy maceration, when the entire syncranium becomes more or less completely disarticulated, the proethmoid and the premaxilla remain in firm contact via an extremely tough bridge of ligamentous tissue (fig. 2). This close association of the two bones suggests the way in which the ascending process may have arisen.

It is sometimes assumed that the development of an ascending process is a necessary concomitant of the development of upper jaw protractility. This assumption certainly is unwarranted. There are many living teleosts in which an ascending process of the premaxilla is well developed but still attached to that bone only by ligament or cartilage, for example, in batrachoidids, lophiids, and ammodytids, and in *Sphyræna vulgaris* according to Allis (1909). Thiele (1963) found that the ascending process in some blenniids is separated from the premaxilla by a distinct line of cartilage. In each of these forms there are also present on the premaxilla an articular process (although it may not be very distinct in blenniids) and a maxillary process, but the upper jaw is significantly protractile only in ammodytids.

Indeed, the presence of ascending, articular, and maxillary processes, and the association of the upper jaw with the cranium through a series of crossing ligaments, have made possible protractility as well as many other special functional improvements of the upper jaw. Evidently, however, the original advantage of this complex upper-jaw system was to provide a mechanism that combined strength with flexibility in fishes of primarily carnivorous habits. This view is supported by the development of a similar system among the more advanced salmoni-

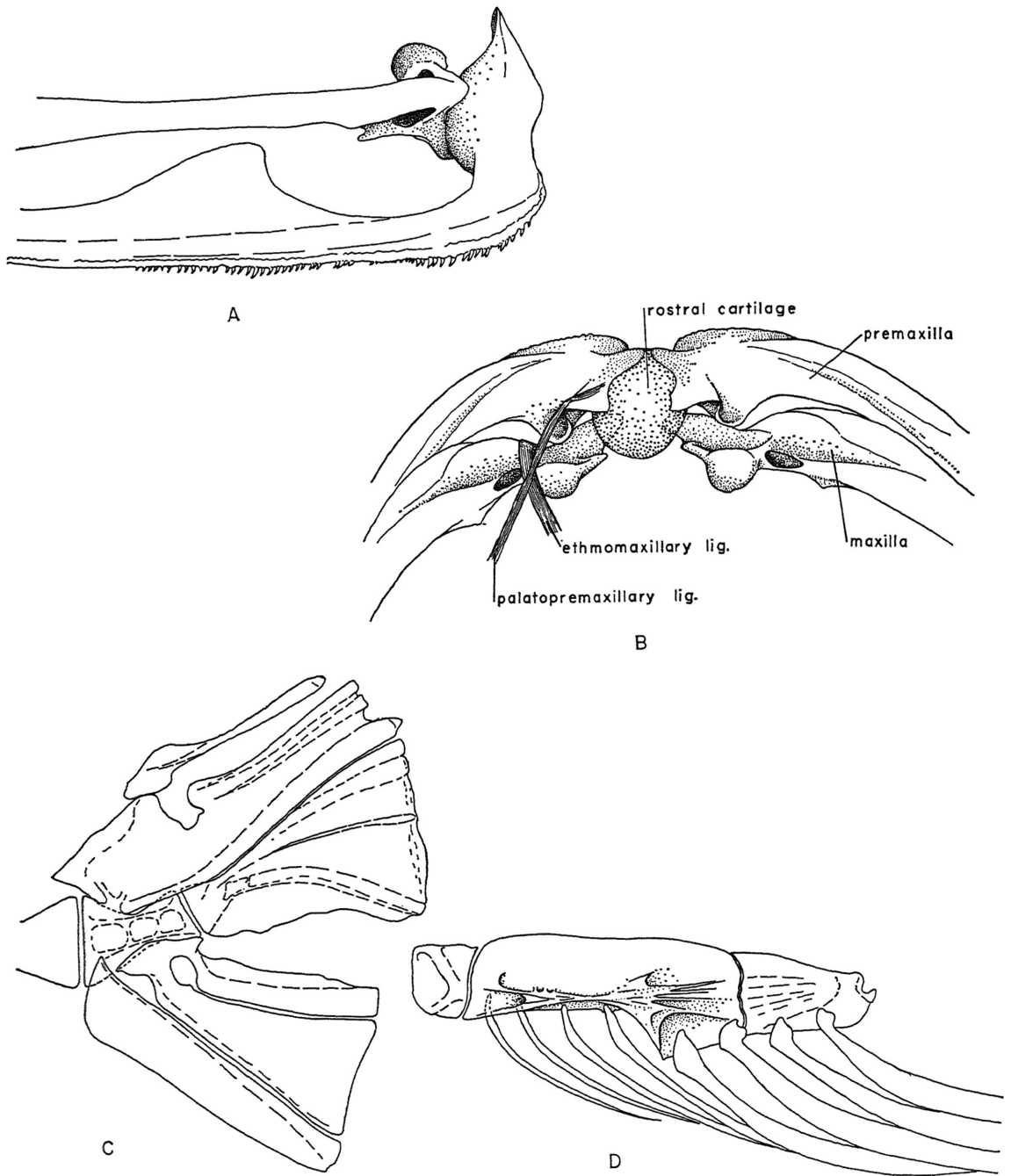


FIG. 3. Details of the skeleton of *Neoscopelus macrolepidotus*. A. Side view of premaxilla and maxilla, anterior to right. B. Dorsal view of upper jaw bones, anterior up. C. Caudal skeleton, anterior to left. D. Hyoid bar and branchiostegal rays, anterior to left.

forms and among the paracanthopterygians. All these fishes are primary carnivores, with essentially non-protractile mouths.

It is of further interest to note that Allis (1909) found in *Salmo* a small, simple articular process together with an "... independent so-called supraethmoid," and he remarked on the similarities in this respect of *Salmo* to *Macrodon* (= *Hoplías*) and *Erythrinus* of the Cypriniformes. He concluded that the "... articular process of the premaxillary of teleosts would thus seem to be as early, or even an earlier acquisition of that bone than the ascending process." Allis was unable, however, to find an undisputed articular process in *Elops* or *Clupea* (Division I) or in *Osteoglossum* (Division II). The occurrence and development of the premaxillary processes may therefore contribute important supplementary evidence for the reality of the Protacanthopterygii, and for the distinctness of the Salmoniformes from other malacopterygian fishes.

In our classification of the Salmoniformes we follow Gosline (1960) in separating the salmonids from the argentinoids, but we further subdivide his Salmonoidei by removing from that assemblage the galaxiids, aplochonids, retropinnids, and salangids. We place the latter families in a coordinate group, the Galaxioidei. This separation emphasizes the fact that galaxiids and their allies have undergone a significant, if small, radiation within the Salmoniformes which is more or less comparable with that of esocoids and that of myctophoids. Among galaxioids, esocoids, and myctophoids there are some very generalized forms and some considerably more advanced ones. In the Galaxiidae, one Chilean species appears to have almost as primitive a caudal skeleton (fig. 4) as does any other malacopterygian group, although its upper-jaw bones are as specialized as those of the most advanced myctophids, i.e., *Brachygalaxias bullocki* has its hypural bones in the caudal skeleton distributed on three more or less distinct centra, but the premaxilla possesses a definite articular process and entirely excludes the maxilla from the gape. Other galaxiids have the hypurals on a single, terminal half-centrum. In their several advanced features, including the complete exclusion of the maxilla from the gape, the galaxiids seem cer-

tainly to have achieved a myctophoid level of organization. Clearly the family and its presumed allies (aplochonids, retropinnids, and salangids) deserve some form of separate taxonomic recognition in contrast to the very much more generalized salmonids.

Whereas the galaxiids have experimented with an advanced upper-jaw mechanism by emphasizing the articular premaxillary process, the esocoids seem to have proceeded along these same lines by developing what could be a very primitive precursor of the ascending process. Esocoid caudal skeletal characteristics are uniformly based on a tri-centrum support of the hypurals. In at least two species the hypurals on each of the last two centra involved tend to become locked together by intervening bone and are in this way strongly reminiscent of the caudal structure typical of all primitive Paracanthopterygii.

Although it is not implied that esocoids may have given rise to paracanthopterygians, it is clear that the Salmoniformes as a group contains, in mosaic occurrence, all the necessary basic specializations to have provided the evolutionary raw materials for all the more advanced groups, including the Ctenothrissiformes, of this superorder. Such, in fact, is the substance of our reasons for the establishment of both the Salmoniformes and the Protacanthopterygii.

When considering the origin of percomorph types, Patterson (1964) evaluated the merits of myctophoids versus the Cretaceous ctenothrissiforms as possible ancestors of the beryciform fishes. He believed that the myctophoids could not have been directly ancestral to the beryciforms "... because their maxilla is not toothed, while maxillary teeth persist in some Berycoidei, and that the Ctenothrissiformes [could not have been] directly ancestral to the group because their post-temporal fossa is not roofed, while a partial roof to the fossa persists in some Berycoidei." Patterson nevertheless concluded that, though no definite decision can be reached without more fossil material, the Ctenothrissiformes are still in every way the most likely ancestors known for the beryciform fishes.

We share Patterson's confidence that the ctenothrissiforms or their close allies, when these become known, will ultimately prove

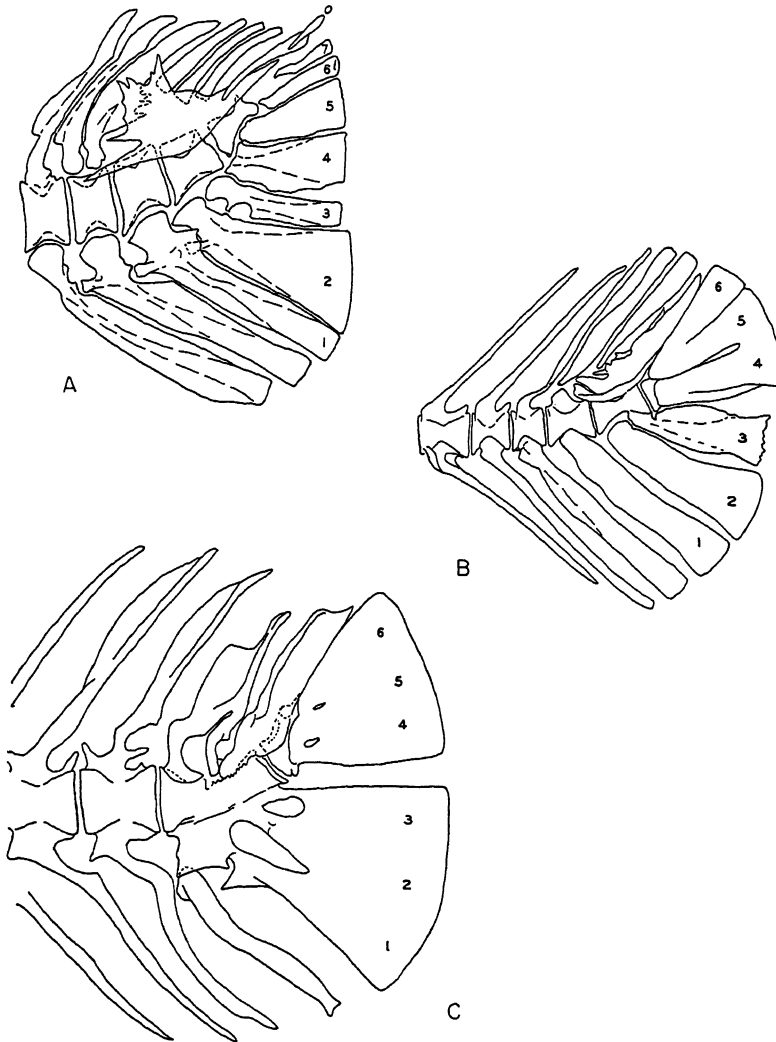


FIG. 4. Degrees of fusion in the caudal fin supports. A. *Salmo gairdneri*.
B. *Umbra limi*. C. *Brachygalaxias bullocki*.

to be ancestral to early acanthopterygians. Not only are the fossil ctenothrissiforms, *Ctenothrissa* and especially *Aulolepis*, remarkably similar in general appearance to primitive beryciforms, as Patterson has so thoroughly illustrated, but one or both of them have in common with some or all beryciforms the following characteristics: two large supramaxillae; a premaxilla with an ascending and an articular process and an alveolar arm that extends below the maxilla; maxillary teeth; ctenoid scales; thoracic pelvic fins; pectoral fins that are elevated on the

sides; a scaly operculum; a caudal fin with 17 branched rays; and a subocular shelf on the infraorbital bones. All these features, save the maxillary teeth, and two of the branched caudal rays, were carried forward into the generalized perciforms. These resemblances leave little doubt of the reality of the phylogenetic connections between the Ctenothrissiformes of this superorder and the Acanthopterygii as here defined.

Another fish discussed by Patterson, the Upper Cretaceous *Sardinioides*, was sufficiently advanced in general structure and

sufficiently similar to the ctenothrissiforms to raise the question in Patterson's mind, and in ours, of the possible role this fish may have played in the evolution of spiny-finned groups. Of *Sardinioides* Patterson wrote: "*Sardinioides* is . . . a very generalized form, approaching the acanthopterygians particularly in the structure on the mouth. From the analysis of acanthopterygian characters made above, three trends in acanthopterygian evolution emerged. The second of these trends, associated with changes in the dentition and the development of a protrusile mouth, is well advanced in *Sardinioides*. The first trend, associated with the use of the pectoral fins in manoeuvring, has not proceeded far. The pectoral fins have migrated on to the flank, the mesocoracoid has been lost, and the pelvic fins have moved forwards (though they have not acquired an articulation with the cleithrum), but the trunk is not deep, the supraoccipital has not begun to separate the parietals, and the post-temporal fossa is still roofed. The third trend . . . has begun with the development of feebly ctenoid scales.

"Two specialized features which might exclude *Sardinioides* from the ancestry of the acanthopterygians are the expanded suboperculum and the reduced ventral postcleithrum, and these characters link the genus with living myctophoids. . . . The adipose dorsal fin of myctophoids [reputed to have been identified in the fossil *Sardinioides*] is a feature which occurs in no acanthopterygians but it is present in one family, the Percopidae."

Added to the above objections to *Sardinioides* as an ancestral type for the beryciforms are the occurrence in *Sardinioides* and in myctophoids of an unusually long alveolar extension of the premaxilla under the maxilla (shorter in all beryciforms), the absence of teeth on the maxilla (present in some Berycoidei), the smallness or absence of the supramaxillae (invariably present and large in beryciforms), and the absence of a subocular shelf (present in beryciforms). None of the above characters separating the myctophoids (and *Sardinioides*) from the beryciforms excludes them from the ancestry of the Paracanthopterygii. In fact, the particular characters by which they differ from the beryci-

forms are the very ones that would be expected to typify the ancestral paracanthopterygian. In short, in paracanthopterygians, the trunk is not deep in most instances, the parietals are not well, or at all, separated, a posttemporal fossa is roofed in numerous species, the suboperculum is usually greatly expanded, the postcleithra are reduced or absent, an adipose fin is present in one family, the alveolar extension of the premaxilla is very long and slender in many species, maxillary teeth are never present, supramaxillae are absent from even the most primitive forms (a minute element may be present in some ophidioids), and a subocular shelf is never present.

In further support of a relationship between the advanced myctophoids and the paracanthopterygians, we have observed the occurrence of levator maxillae superioris muscles in the jaw mechanism of some myctophids and a type of caudal skeleton with dual-centrum support of the hypurals in *Neoscopelus* (fig. 3) that almost certainly must have been antecedent to the extremely characteristic caudal skeleton of primitive Paracanthopterygii (see discussion below, under Paracanthopterygii).

Hence, we concur with Patterson that the Ctenothrissiformes, or their near allies as yet undiscovered, must have been ancestral to the Acanthopterygii (as defined here), but we propose that Cretaceous myctophoids such as *Sardinioides* may well have produced a parallel spiny-finned radiation which we recognize as the Paracanthopterygii.

Finally, we do not relate the ctenothrissiforms to the clupeoid fishes, as has often been done. Rather, we link them with some early group of myctophoid-like salmoniform fishes in which the supramaxillae were not reduced, the premaxilla had not excluded the maxilla from the gape, and in which the adipose dorsal fin had disappeared. The combined trends to develop a complex upper jaw with articular and ascending processes, to elevate the pectoral fin on the flank, and to advance the pelvic fins to a position under the pectorals seem to be a peculiarly protacanthopterygian constellation of characters that is not known in any clupeoid. Moreover, all clupeiforms, even the most primitive (*Denticeps*), possess the highly distinctive combination of an oto-

physic connection, opercular lateral-line canals, and a cranial recessus lateralis that sets these fishes entirely apart and excludes them from the ancestry of other teleosts.

PROBLEMATICAL SUBORDERS OF THE
ORDER SALMONIFORMES

SUBORDER STOMIATOIDEI: Stomiatooids are pelagic and bathypelagic fishes of uncertain affinities. Regan (1923) considered them to be related to clupeoids. Garstang (1931) and Beebe and Crane (1939) suggested that they may have relationships with salmonoids. Stomiatooids are characterized by photophores, a large basisphenoid associated with the absence of lateral prootic walls in the anterior region of the posterior myodome (see fig. 5), preopercular and infraorbital lateral-line canals connected by the supraorbital canal in the frontal, often a dorsal and in some cases a ventral adipose fin, and a mesocoracoid in those members with well-developed pectoral fins. Like many clupeoids, but also salmonoids, stomiatooids tend to have bony denticles or teeth along the ventral border of the maxilla, and well-developed supramaxillae are present in the less specialized members. Unlike clupeoids, stomiatooids do not have a close approximation of infraorbital

and preopercular canals nor do they have a clupeomorph type of ear-swim-bladder connection. Several skull characters, such as a large basisphenoid, the shape and relations of the pterotic and epiotic bones, and the large amount of skull cartilage suggest relations with salmonoids. However, the caudal skeleton of stomiatooids is more specialized than that of generalized salmonoids but similar to that of the most advanced members of the Salmonoidei.

Among the several trends in the stomiatooids is the elongation of the body, even in the relatively unspecialized Gonostomatidae. The Sternoptychidae are exceptional in having a body that is extremely compressed and deep. There is a marked tendency toward reduced ossification in one or more of the vertebrae immediately posterior to the skull. Even in many relatively unspecialized gonostomatids and astronesthids, the cranium is attached to the vertebral column by relatively long and extremely tough but flexible ligaments. In the Astronesthidae and Melanostomiidae the trend toward elongate body form is associated with a reduction in pectoral fin size. In many of the more predaceous groups (Gymnophotodermi and Lepidophotodermi of Parr) the gill rakers have been replaced by teeth, and long, canine-like, de-

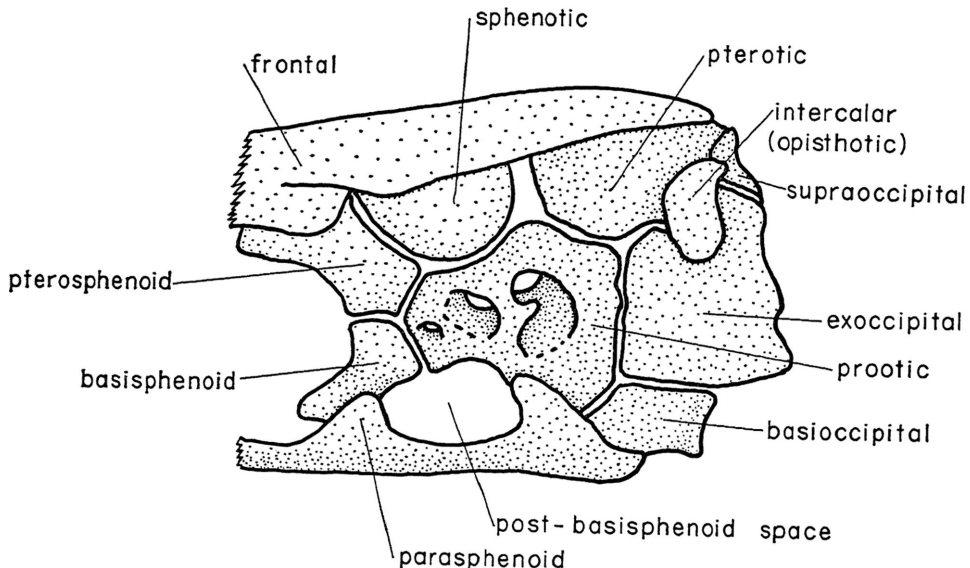


FIG. 5. Lateral view of the posterior part of the cranium of *Astronesthes niger*, anterior to left.

pressable teeth have developed in the jaws. The most specialized of the many modified jaw mechanisms that occur in this suborder is to be found in *Malacosteus* (see Günther and Deckert, 1959). Deep-water forms are weakly ossified, while surface-water species are moderately bony. A tendency to lose the parietal bones recurs in some groups.

Stomiatooids may be divided into two or perhaps three groups, the first containing the generalized, scaled Gonostomatidae and a specialized offshoot of the latter family, the Sternoptychidae. Hubbs (1953) suggested uniting the Gonostomatidae and the Sternoptychidae. Considering the close relationship between some gonostomatids and sternoptychids noted by Gregory and Conrad (1936) and accepted by Rechnitzer and Böhlke (1958), we suspect that a study of the morphology of these fishes will support Hubbs's suggested merger. The remaining families appear to be interrelated on the basis of skull characters and in the frequent occurrence of a mental barbel. Furthermore, most of the included species are without scales. Parr (1927, 1930) proposed to separate the stomiatooids into three suborders, the Heterophotodermi [=Gonostomatoidea] containing the Gonostomatidae and Sternoptychidae, the Lepidophotodermi [=Stomiatoidea], including the apparently scaled Stomiidae and the Chauliodontidae, and the Gymnophotodermi [=Astronesthoidea] for the remaining, scaleless families. Beebe and Crane (1939) and Berg (1940) recognized these groups as superfamilies. The distinction between the Stomiatoidea and the Astronesthoidea remains problematical. Such a separation was not recognized by Regan and Trewavas (1930) even though outlined by Parr (1927).

Important works of relatively recent date on the morphology and classification of stomiatooids are: Regan and Trewavas (1929) on the Astronesthidae and the Chauliodontidae; Regan and Trewavas (1930) on the Stomiidae, Melanostomiidae, and Malacosteidae; Parr (1927) on the Melanostomiidae; Norman (1930) on the Gonostomatidae and Sternoptychidae; Ege (1934, 1948) on the Stomiidae and Chauliodontidae, respectively; Beebe (1934) on the Idiacanthidae; Parr (1937) on the Sternoptychidae; Schultz (1961) on the Sternoptychidae; Beebe and

Crane (1939) on the Melanostomiidae; and Grey (1960) on the Gonostomatidae. A few important papers on functional morphology have been published, for example, those of Tchernavin (1953) on the feeding mechanism of *Chauliodus*, Günther and Deckert (1955) on the functional morphology of the jaws and breathing apparatus of several stomiatoids, and Günther and Deckert (1959) on the function of the jaw apparatus in *Malacosteus* and *Photostomias*.

SUBORDER ALEPOCEPHALOIDEI: There is little critical anatomical information on the Alepocephalidae, and any decision concerning their taxonomic position must therefore be considered tentative.

On the basis of syncranial architecture and caudal fin skeleton, the Alepocephalidae cannot be included in the Clupeomorpha as here restricted, nor, on these same characters, can they be shown to resemble the Elopomorpha.

The Alepocephalidae differ mainly from the families of the Clupeomorpha in the absence of an otophysic connection (swim bladder not developed) or remnants of such a connection, in the neurocranium (no temporal or pre-epiotic fossae, no auditory fenestrae), and in the caudal fin skeleton (see Gosline, 1960). In the alepocephalids, the caudal fin skeleton has a distinct first uroneural (not fused with or wedged into a centrum), three distinct centra, and a second hypural that articulates with a centrum and is not free as it is in all clupeomorphs except the extremely primitive Denticipitoidei.

At least in *Alepocephalus*, and unlike the Clupeomorpha, the parapophyses are fused with the centra, and only the last haemal arch is autogenous. In this genus, too, the foramina associated with the pars jugularis show an advanced condition, namely, one in which there are no separate openings for entry of the head vein and the orbital artery.

The most noticeable difference between the Alepocephalidae and the Elopiformes lies in the syncranium, particularly in the palatoquadrate arch and in the branchial skeleton (teeth occur only on the palatine and ectopterygoid in *Alepocephalus*); there are several differences in the occipital region of the skull and in the jaws (no posttemporal or subtemporal fossae, no bulla in the intercalar, parietals widely separated, no separate entrances

for the head vein and orbital artery, premaxilla contributing appreciably to the gape). The caudal fin skeleton of *Alepocephalus* approaches that of the elopiforms, but differs in many details.

Taken in sum, the characteristics of the Alepocephalidae do not suggest close relationships with any group of Division I.

By contrast, we cannot find any trenchant characters to separate the Alepocephalidae from the Salmoniformes of Division III. The skull does show points of difference, but the degree of differentiation is considerably less than that existing between the alepocephalids and Division-I fishes. The skull of *Alepocephalus* could, indeed, be derived from a basic salmoniform type. Interpretation of the alepocephalid skull is made somewhat difficult by the probability of its showing adaptive responses to the deep-sea environment. The caudal fin skeleton of alepocephalids is basically like that of the "primitive" salmoniform type, e.g., *Salvelinus*. The differences in the caudal skeleton between the alepocephalids and the salmoniforms are considerably fewer than those between the clupeomorphs and elopomorphs. The caudal skeleton of *Alepocephalus* shows greater affinity with the salmoniform type than it does with the other primitive types of caudal skeleton found in *Esox*, *Hiodon*, and *Denticeps*.

Because so little is known about the anatomy of the Alepocephalidae, we are unable even to suggest their affinity with any particular group of the Salmoniformes. Since there are known differences between the Alepocephalidae and the Salmonoidei, we propose that, at least for the time being, the alepocephalids be recognized as a suborder (Alepocephaloidei) of the Salmoniformes.

Regan (1929), Jordan (1923), Berg (1940), and Norman (in his "Draft Synopsis") all referred the Alepocephalidae to the suborder Clupeoidei, although Berg, (1940, p. 431) commented that the Stomiatoidei were "... especially near the Alepocephalidae." Bertin and Arambourg (1958) also commented on alepocephalid-stomiatoid resemblances, but placed the former in a distinct suborder (Alepocephaloidei) of their Clupeiformes. Earlier, Garstang (1931) treated the alepocephalids as a group coordinate with the salmonoids, another group termed the Lam-

padephorii which contained the stomiatoids and scopeloids, and yet another group which comprised only the esocoids. Gregory (1933) actually lumped the alepocephalids and stomiatoids in a single suborder of the Isospondyli. Obviously, much more research is needed before the status of the Alepocephaloidei is understood.

Parr is engaged in revisional studies of the alepocephalids (Parr, 1951, 1952) and has published a complete review of the Searsiidae (Parr, 1960), a group that we do not for the present recognize as of familial rank.

SIGNIFICANCE OF ORDER GONORYNCHIFORMES IN HISTORY OF OSTARIOPHYSAN FISHES

Fishes now grouped in this order have had a checkered taxonomic history.

The history of *Chanos* may be summarized as follows: in 1775 Forskål first described a specimen of *Chanos* as a *Mugil*; Richardson (1843) placed it in the genus *Leuciscus*. *Chanos* was placed, with *Gonorynchus*, in a category of intermediate Malacopterygii by Valenciennes (1846). Günther (1868) considered *Chanos* to be a member of the Clupeidae, but this view was not accepted by Kner (1869), Cope (1871), or Gill (1872) who considered *Chanos* as representing a distinct family separated from the Clupeidae. Near the turn of the century, Woodward (1901) placed *Chanos* in the Albulidae, a move that has never received support from other ichthyologists. At about the same time Ridewood's osteological studies (1904a, 1905c) clearly demonstrated that *Chanos* and *Albula* were not related and led him to the supposition that, although *Chanos* was not a clupeid, it should be considered a clupeoid fish. He also pointed out the resemblances between *Chanos* and *Phractolaemus* and suggested their relationship (a move amply borne out by the recent work of Thys van den Audenaerde, 1961). In his classification of 1923, Jordan included *Chanos*, together with *Gonorynchus*, *Phractolaemus*, *Kneria*, and *Cromeria*, in the suborder Clupeoidei, but so arranged that *Cromeria* was distantly separated from the other genera. This conclusion, with regard to *Chanos* as a clupeoid fish, is essentially similar to Jordan's earlier (1905) views, but it is interesting to note that in that book Jordan

commented on the superficial resemblances between *Chanos* and a dace.

Regan (1929) followed an essentially similar arrangement, associating *Chanos* and *Cromeria* with *Kneria* among the clupeoid fishes, but placed *Gonorynchus* near the Mormyridae (although in 1909 he suspected a relationship between *Gonorynchus* and *Kneria*). Myers (1938) suggested that *Cromeria* might be a larval *Kneria*. In Berg's 1940 classification *Chanos* and *Kneria* are included in the clupeiform suborder Chanoidei, whereas *Phractolaemus* and *Cromeria* are each given subordinal status but retained near the Chanoidei; *Gonorynchus* is also given subordinal rank but is placed, without comment, between the Opisthoproctoidei and Notopteroidei. Bertin and Arambourg (1958) united *Chanos*, *Kneria*, and *Phractolaemus* within a single clupeiform suborder (Chanoidei), but they kept separate suborders for *Cromeria* and *Gonorynchus*. Gosline (1960) was the first author to suggest a probable relationship among all five genera, but he stressed the very loose nature of their relationships by recognizing five superfamilies within his suborder Gonorynchoidei. A recent paper dealing with *Chanos*, *Kneria*, *Cromeria*, and *Phractolaemus* (d'Aubenton, 1961) considered the problems of their relationships but reached no definite conclusion. Most recently Géry (1964) has described a new family, genus, and species of *Kneria*-like fish from African fresh waters (family Grasseichthyidae). We had previously studied this fish and concluded that it must be included in the Kneriidae. Anatomically it links *Kneria* with *Cromeria*, differing from each, however, mainly in the absence of epipleural and cranial ribs. Because we (Greenwood and Rosen) have not yet published our anatomical findings on *Grasseichthys*, we prefer not to consider the genus further in this paper.

Although we agree in essence with Gosline that the gonorynchoid fishes are more closely related to one another than any of them is to other fishes, we think that *Chanos*, *Kneria*, *Cromeria*, and *Phractolaemus* form a close-knit and natural assemblage in which at least *Kneria* and *Cromeria* must be united in a family Kneriidae. *Gonorynchus* is certainly the most divergent member of this group, but is nonetheless tied in with *Chanos*, *Kneria*,

Cromeria, and *Phractolaemus* by many of the same characters that closely unite those four genera. All five have in common a supra-branchial organ, upper and lower intermuscular bones, toothless jaws in which the premaxilla is either a thin splint or scalelike bone, and a caudal skeleton with the uroneural and lowermost hypural forming a V-shaped wedge around four or five smaller hypural elements. The whole unit stems from a terminal half-centrum. Suggestive also of relationship among the genera is the development of a protractile upper jaw and an extremely delicate, loosely articulated, palatopterygoid suspension in *Gonorynchus*, *Kneria*, *Cromeria*, and *Phractolaemus*. The mouth is superior in *Phractolaemus*, inferior and below a projecting snout in *Gonorynchus*, *Kneria*, and *Cromeria*. In *Chanos* the mouth is terminal, non-protractile, and has a firmer and more heavily ossified suspension.

Other similarities among the genera have a distinctly mosaic distribution. For example, the infraorbital and preopercular canals of the cephalic lateral-line system are similar and widely separated in all, but only in *Chanos*, *Kneria* (fig. 6), and *Phractolaemus* does a suprapreopercular bone develop. In contrast, a supratemporal commissure is present in the cephalic lateral-line system (fig. 6) of all genera save *Cromeria*. On the other hand, a fifth ossified basibranchial occurs between the enlarged ceratobranchials of the fifth gill arch (tooth-bearing lower pharyngeal bones) only in kneriids (fig. 7), and the swim bladder is divided in *Chanos* and *Kneria*, simple in *Cromeria*, respiratory in *Phractolaemus*, and absent from *Gonorynchus*. In *Chanos* and *Kneria* the division results from a constriction of the swim bladder near the origin of the ductus pneumaticus as in the cypriniform fishes.

The most impressive, and perhaps phylogenetically the most significant, similarity among the gonorynchiform genera is the presence of one or more cephalic ribs associated with the specialized first three cervical vertebrae. In *Gonorynchus* there is a single, delicate, partly ligamentous rib on a posterior ledge of the exoccipital. Each of the first three vertebrae is peculiarly modified and different from its fellows (fig. 8). The third is especially differentiated; it possesses a deep ex-

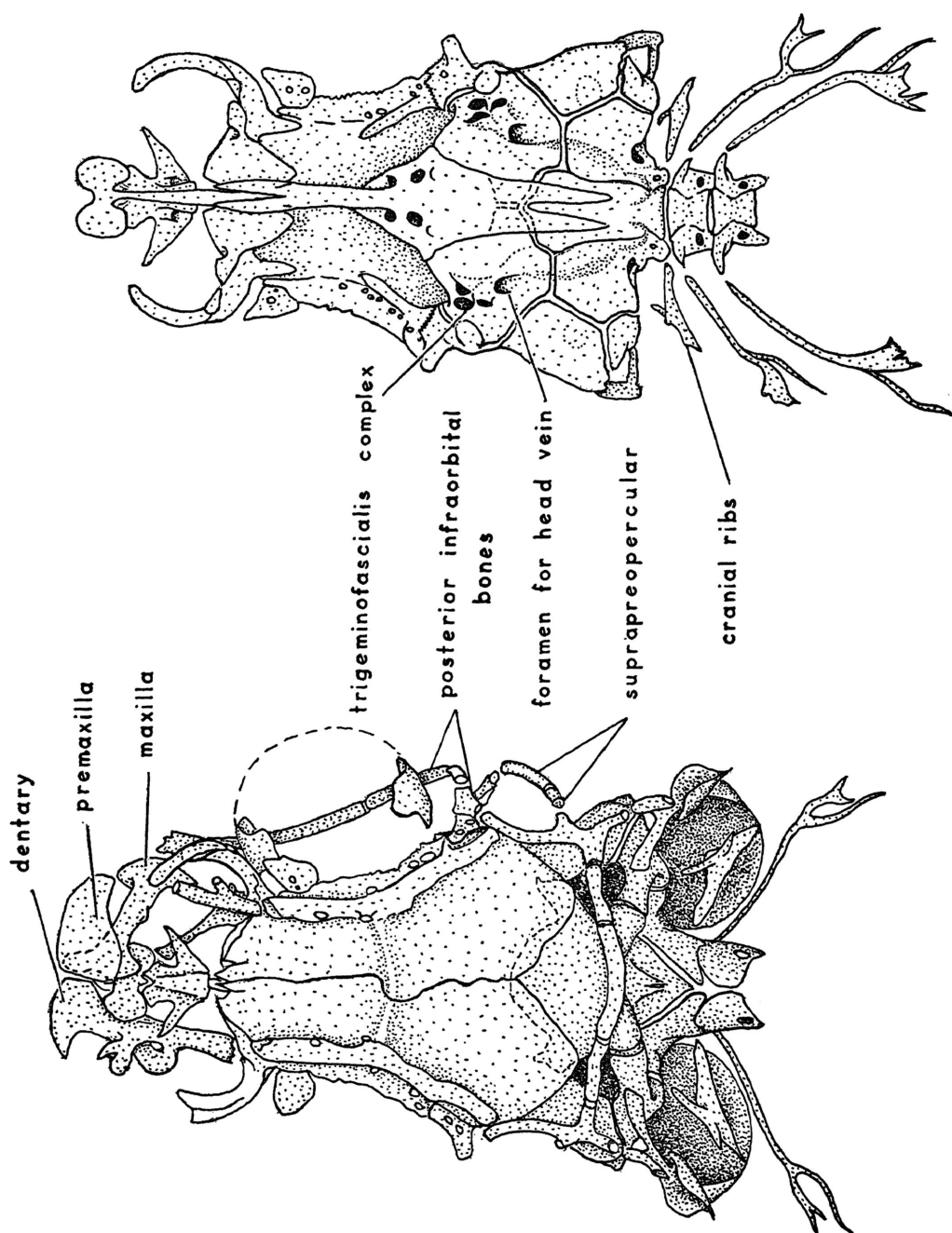


FIG. 6. Neurocranium, upper jaw elements, and the first two vertebrae of *Xneria witei*. Note the "cranial ribs" associated with the skull and first vertebra. *Left*: Dorsal aspect. *Right*: Ventral aspect (upper jaw elements excluded).

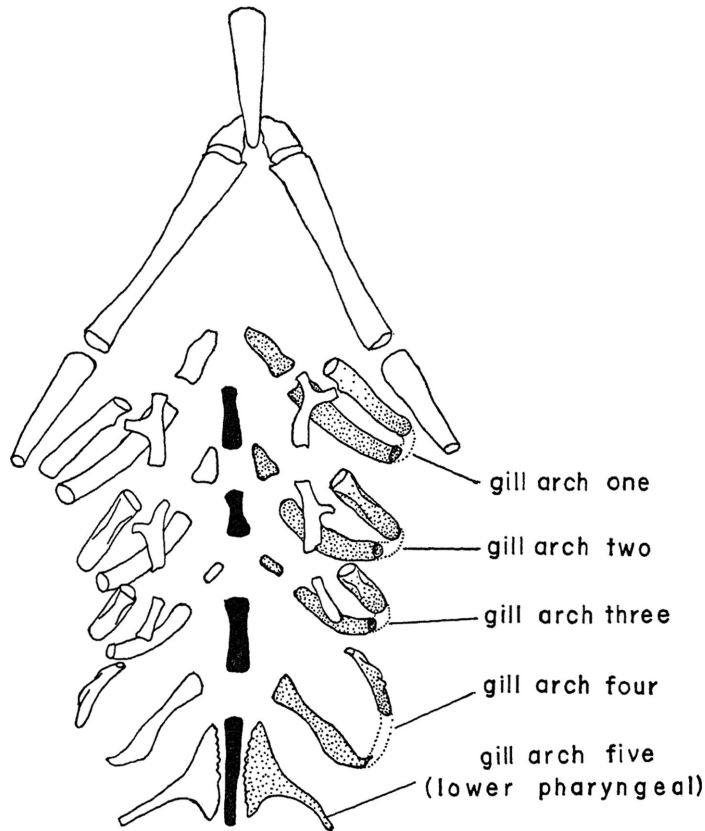


FIG. 7. Pharyngobranchial skeleton of *Grasseichthys*, in dorsal view. Note the well-ossified fifth basibranchial (in black) lying between the lower pharyngeal bones.

cavation for the head of a large riblike bone bearing a posterodorsal flange. The normal complement of pleural, epipleural, and epineural ribs occurs first on the fourth vertebra. Epineurals and true ribs are not present anterior to the fourth vertebra.

In *Chanos* there is an arrangement of ribs, muscles, and connective tissue in the occipito-cervical region, which, because of their association with the swim bladder, suggests an indirect otophysic connection. The first cephalic rib extends posterolaterally to the ligamentous extension of the long pterotic process; from this point it gains additional support from a ligament that extends anteriorly to the pterotic proper. This first rib bends posteriorly where it meets the pterotic process and thence grades insensibly into a delicate splint which merges with the fascia of the epaxial muscles. A second, much larger, ce-

phalic rib originates partly on the basioccipital and partly on the closely associated first vertebra. It passes backward parallel to the first cephalic rib and meets a further extension of the pterotic process on the upper edge of the cleithrum. Halfway along its length, a prominence arises on the upper surface of the second cephalic rib, from which point a broad strap of muscle extends forward to the exoccipital. From the posterior margin of this rib a sheet of connective passes backward to the anterior edge of the first, and unusually large, pleural, or true, rib on the third vertebra. The second cephalic and first pleural ribs are united further by a pair of modified, obliquely crossing, superficial, intercostal muscles that lie over the connective tissue sheet. Underneath this sheet a small muscle arises proximally on the first pleural rib and passes forward to the occipital region. The complex sys-

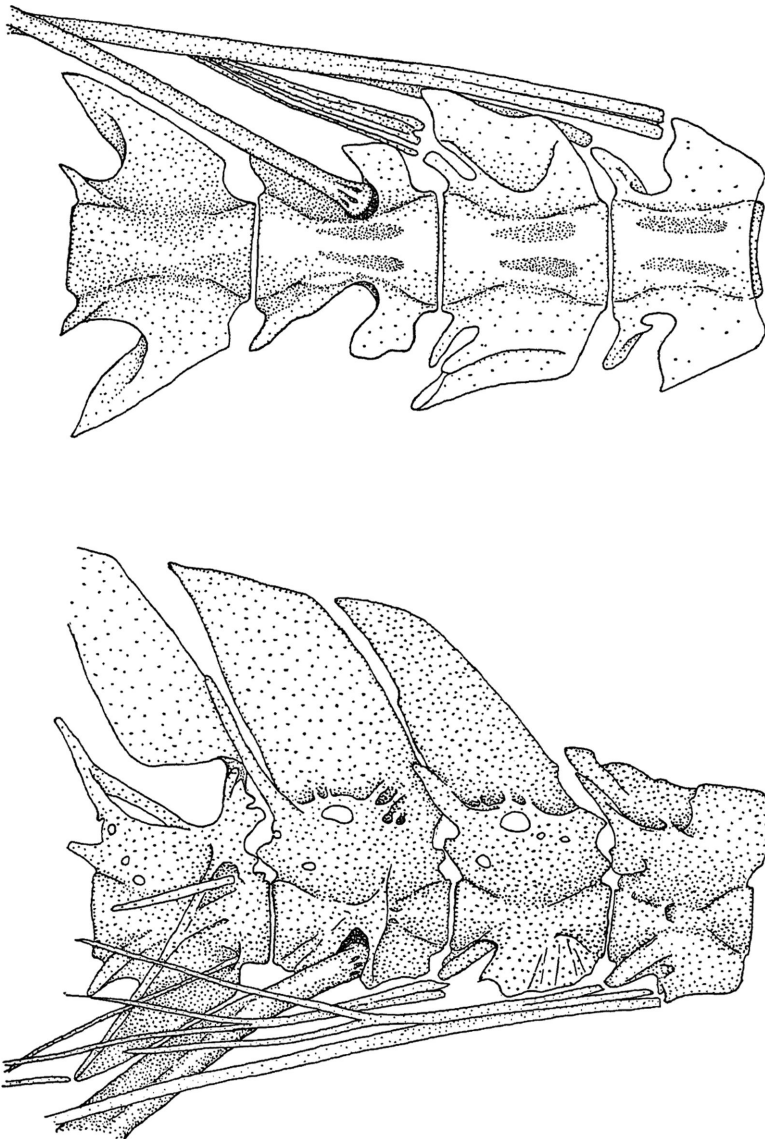


FIG. 8. The first four vertebrae of *Gonorynchus gonorynchus*, showing the peculiarly modified and movable riblike bone of the third vertebra. Note also that the third vertebra is smaller than vertebrae in front of and behind it, and that the fourth vertebra is the first to have a full complement of ribs. *Top*: Ventral aspect. *Bottom*: Lateral aspect.

tem described above is especially interesting in view of the fact that in *Chanos* the first pleural is firmly in contact with the upper surface of the anterior chamber of the swim bladder, as in cypriniform fishes. In addition, as in certain Cypriniformes, there is in the occipital region of *Chanos* a large, and

very deep, post-temporal fossa; medial to this is a small fenestration bounded by supra-occipital, exoccipital, and epiotic bones. The occipitocervical complex of *Chanos* has, in fact, the appearance of an arrangement that could precede the development of a series of ossicles like those of the Weberian apparatus.

Other cypriniform-like characters of *Chanos* are the transversely subdivided swim bladder, the form of the dorsicranium, mouth parts, and caudal skeleton, and the general dace-like appearance and behavior of the fish as noted by Jordan (1905) and others.

Chanos-like occipitocervical modifications occur in *Kneria* (although the two cephalic ribs are fused together) in which a chambered swim bladder also is present. In *Cromeria*, a simple, delicate cephalic rib is present, and in *Phractolaemus* the single cephalic rib is large and in the position of the second cephalic rib of *Chanos* which it resembles.

The species of *Kneria*, *Cromeria*, and *Phractolaemus* occur only in the fresh waters of tropical Africa. *Chanos* is known from salt, brackish, or fresh water on both sides of the Pacific. *Gonorynchus* now occurs only in the Indo-Pacific and, so far as is known, never enters fresh water. Both of the latter genera, or at least their close allies, however, are known from Middle Eocene fresh-water deposits in North America.

The phyletic relationships of the Gonorynchiformes are uncertain, but they show affinity with both the Salmoniformes and the Ostariophysi, especially the Characoidei. Despite the fact that several "primitive" characters are preserved in some members of the order, there are many other characters that demonstrate its membership in our Division III. Among the latter may be mentioned the high degree of consolidation in the caudal fin skeleton (higher, indeed, than in many Salmoniformes), the specialized jaw structure (especially the loss of supramaxillae and the evolution of a protrusile mouth), and the peculiar occipitocervical modifications (particularly the "cranial" ribs) often associated with the constriction of the swim bladder into distinct anterior and posterior chambers. The vertebral column also shows "advanced" characteristics; in only one genus (*Chanos*) are the parapophyses autogenous, the remaining genera having the parapophyses either fused with the centra (*Kneria* and *Gonorynchus*) or, apparently, wanting (*Phractolaemus*). By contrast, upper and lower intermuscular bones are present in all genera except *Grasseichthys* in which neither type of intermuscular bone is developed.

Those characteristics that suggest some af-

finity with the Ostariophysi are the caudal fin skeleton, the occipitocervical specializations, and the trend toward a divided swim bladder. In our opinion, the resemblances between the two groups suggest their derivation from a common stem, the dichotomy being very near the base. The stem itself was probably derived from some ancestral salmoniform.

The caudal skeleton of the Gonorynchiformes, with its well-defined, V-shaped boundary (see above, p. 375, and Gosline, 1960, fig. 8) is essentially that of the characoids and cyprinoids.

The occipitocervical modifications are described in detail above. The most complex condition of both this region and the swim bladder occurs in *Chanos*, a genus that otherwise shows the greatest aggregation of "primitive" characters. Next to *Chanos*, the occipitocervical modifications of *Kneria* are the most complex, with *Phractolaemus* and *Cromeria* showing a much simpler condition. The picture presented by *Gonorynchus* is also one of simplification; there is only one pair of cranial ribs and the swim bladder is wanting; however, in this genus there is a peculiar modification of the pleural rib of the third vertebra as described above. The general impression gained from these fishes is one of possible preadaptation for the involvement of vertebral and neurocranial elements in the ultimate development of a complex otophysic connection.

There is some similarity between the dorsicranial architecture of certain gonorynchiform fishes (especially *Chanos*, *Kneria*, and *Phractolaemus*) and that of the characoid Cypriniformes. Basically the cranial lateral-line canal system is similar in both groups, a noteworthy resemblance being the presence of a well-developed supratemporal cross commissure. The canal systems differ, however, in that there is no parietal branch of the supra-orbital canal in the Gonorynchiformes, nor is an epiphyseal branch developed on the frontal in these fishes, although the supraorbital branch in *Kneria* bends inward at the epiphyseal position. These canals are usually present in the ostariophysans. A suprapreoperculum carrying the dorsalmost part of the preopercular canal is developed in both groups.

Resemblances between the Gonorynchiformes and the Ostariophysi also occur in the

occipital region of the skull and in the palatopterygoid arch. A posttemporal fossa is present in *Kneria* (shallow), *Phractolaemus* (moderately deep), and *Chanos* (deep), and in all Gonorynchiformes the supraoccipital is a broad-based and extensive bone. In no gonorynchiform, however, is the posttemporal fossa divided by a transverse limb of the epiotic.

Little guidance on the relationships of the Gonorynchiformes can be obtained from jaw structure, because all genera except *Chanos* and *Kneria* show either a marked reduction and simplification of the jaw elements or, as in *Phractolaemus*, a highly specialized condition. There is some resemblance between the jaw of *Chanos* and that of *Cyprinus*, particularly in the form of the dentary and the maxilla.

As far as can be determined the jaw is protrusible in all except *Chanos*, and extremely protrusile in *Kneria* and *Gonorynchus*, both of which have inferior mouths. The mouth of *Phractolaemus* is superior and highly extensible, that of *Cromeria* subterminal.

In the palatopterygoid arch of the Gonorynchiformes there is only slight contact between the metapterygoid and quadrate, or no contact at all, thus recalling the fenestra between the quadrate and metapterygoid which is so characteristic of the Characidae (*sensu* Weitzman, 1962) and at least some primitive Cyprinidae (e.g., *Opsariichthys*).

The absence of intracranial swim-bladder diverticula, as well as the characters discussed above, clearly serves to exclude the Gonorynchiformes from the clupeoid fishes (Clupeomorpha as here defined) with which at least some of its members (particularly *Chanos*) have been associated in the past.

Chanos (see Woodward, 1901) has been linked with the Albulidae, but a detailed consideration of syncranial characters, branchial skeleton, and caudal fin skeletons leaves little to support such an alliance. A few details are, it is admitted, shared by *Chanos*, *Kneria*, and *Phractolaemus* on the one hand and *Albula*, *Elops*, and *Megalops* on the other. These include posttemporal fossae, a supratemporal cross commissure in the cephalic lateral-line system and a parasphenoid which does not extend beneath the whole length of the basioccipital. These characters, however, are also common to the Cypriniformes, which in ad-

dition share with the Elopomorpha (but not with the Gonorynchiformes) a parietal branch of the supraorbital canal, subtemporal fossae, and orbitosphenoids. In *Chanos* there is a peculiar canal on the inner aspect of the premaxilla. The possible homology of this canal with the apparently unique premaxillary canal in the Albulidae (see Gosline, 1961) has been investigated. In *Chanos*, however, the canal houses part of an interpremaxillary ligament.

Gonorynchus is even less like an albuloid, as was clearly demonstrated by Ridewood (1905c). The persistence in certain gonorynchiforms and ostariophysans of elopoid and albuloid characters (and, for that matter, of some osteoglossomorph characters also) is yet another example of the way in which presumably primitive structures inherited from ancestral holostean stocks are retained in groups otherwise far removed from one another in the teleostean radiation.

Boulenger (1904) considered the Phractolaemidae to be most closely related to the Osteoglossidae, but, as Thys van den Audenaerde (1961) has shown, there are more differences than resemblances between the two families, particularly in jaw structure, the palatopterygoid arch, and the morphology of the dorsicranium. Similarly, there are but few shared characteristics between the gonorynchiform fishes and the Osteoglossidae or, for that matter, the Osteoglossomorpha as a whole.

Important papers on the anatomy and taxonomy of the Gonorynchiformes are the classic studies of Ridewood on *Chanos* (1905a), *Phractolaemus* (1905b), and *Gonorynchus* (1905c), and of Swinnerton (1903) on *Cromeria*. Recently there have been papers by Thys van den Audenaerde (1961) on *Phractolaemus*, Gosline (1960) on the *Kneriidae*, *Gonorynchidae*, *Chanidae*, and *Cromeriidae*, and d'Aubenton (1961) on *Cromeria*. Giltay's (1934) anatomical studies on *Kneria* are, unfortunately, marred by certain inaccuracies (especially in his description of the cranium) but remain the only detailed accounts of this genus.

SUPERORDER OSTARIOPHYSI

This group, consisting of some 5000 to 6000 known species, constitutes the majority of fresh-water fishes and is represented on

all major land masses except Greenland and Antarctica. Although the group as a whole is a predominantly fresh-water one, a few catfish families (Ariidae, Aspredinidae, and Plotosidae) contain a large percentage of marine species. Ostariophysans are of diverse habits and form and include characoids, gymnotoid "eels," carps and minnows, suckers, hillstream fishes, and catfishes. They occupy a wide variety of habitats and trophic niches. Some of the species are well-toothed, predatory types, and others are omnivorous or vegetarian. Some of the most specialized forms are the toothless detritus and microphagous species. The Characoidei, Cyprinoidei, and Siluriformes each have blind, cavernicolous representatives. Despite the great morphological diversity of these fishes, all possess a distinctive kind of otophysic connection, the Weberian apparatus.

Unfortunately the fossil record tells us almost nothing about the origin and early distribution of these fishes. Virtually all of them are primary fresh-water fishes (Myers, 1938), so that we cannot envisage a marine origin for the group. The earliest fossils that can with assurance be identified as ostariophysans are of Tertiary age. However, the group is undoubtedly much older, for all known fossil ostariophysans are very similar to Recent species, and a very long period must have been required for the initial differentiation of the two contained orders. The relationships of the Ostariophysii are discussed in connection with the Gonorynchiformes (see above). We do not subscribe to the theory promoted by Hoedeman (1960) that "... the Ostariophysans [stand] at the very beginning of teleostean phylogeny, starting with ancestors of the modern Siluriform series." We also believe that the ostariophysans are relatively primitive teleosts, but the evidence clearly indicates that characoids are more generalized than siluriforms. Moreover, we cannot see how a group of fishes with such a specialization as the Weberian apparatus could possibly be ancestral to any other teleosts.

The distribution of Recent and fossil ostariophysans is of great zoogeographical interest and importance. Recent and fossil characoids (Weitzman, 1960a, 1960b) are virtually confined to Africa and to South America, and it appears probable that most, if not all, of their evolution must have taken place

on these continents. Siluriformes, although not confined to these continents, exhibit their greatest diversity there; in addition, the most primitive living catfishes are confined to southern and western South America where they are isolated as relicts. Hence, it seems likely that catfishes evolved in the South American and African tropics. On the other hand, the cyprinoids have their greatest diversity in southeast Asia and may have arisen there from some characoid-like ancestor. The gymnotoids are confined to South America and unquestionably evolved there from characoids. Regan (1922) presupposed a South Atlantic bridge to explain the distribution of the Ostariophysii. At times this theory has been rejected by most biologists (e.g., Darlington, 1957) as well as by geophysicists, and all evidence points against any Cenozoic connection between the two continents. Piton (1938) described some fossils from the Eocene of France and considered them characoids, thereby apparently extending the range of this group. An apparent range extension into the Holarctic seemed to make an Afro-Asian origin of characoids more feasible. However, Weitzman (1960a) demonstrated that Piton's fossils are not characoids but that they are salmonoid or perhaps esocoid relatives (Thaumaturidae) and that characoids are confined to Africa, South America, and Middle America northward in North America to the Rio Grande. The implications of this pattern of distribution are being reinvestigated in the light of recent geophysical evidence which indicates that continental drift may indeed have occurred (Myers, in press). If such earth movements took place and the time of the origin of this movement can be dated, and if the characoids have always been confined to the neotropics and Africa, it follows that the Cypriniformes may have originated prior to the time when Africa and South America separated finally. The apparent absence of valid pre-Cenozoic fossil ostariophysans does not, however, preclude their existence. The Mesozoic fresh-water fossil deposits in Africa and South America have been little investigated for fish remains, and, if Mesozoic ostariophysans existed, it is in those areas that they should be found.

The Weberian apparatus has been the subject of a great many papers, of which the most important are cited by Alexander (1962,

1964a, and 1964b). The apparatus consists of four or more supporting anterior vertebrae (pars sustentaculum) and three, and in some cases four, small, movable, bony parts connected to the internal ear (pars auditum). The movable bony parts are the tripus, intercalarium, scaphium, and claustrum. A chamber, the sinus cavum imparis, is joined posteriorly and, below the foramen magnum, with the claustrum and scaphium. This chamber is filled with fluid and is roofed by inwardly directed exoccipital lamellae, and it rests on the dorsal inner surface of the basioccipital.

The Weberian apparatus, present in all Ostariophysi, is modified in many diverse and specific ways, some of which are diagnostic of orders, families, and other groups. Superficially similar modifications of the apparatus have been attained through convergence in such unrelated ostariophysans as the bottom-dwelling loaches and catfishes.

The claustrum and intercalarium tend to be lost from the pars auditum independently in members of several families, and there is a distinct tendency in bottom-dwelling forms for the normally two-chambered swim bladder to be reduced and enclosed in a bony capsule. There is also a distinct tendency for centra of the Weberian vertebrae to ankylose and for additional vertebrae to be incorporated into the apparatus.

Several other phylogenetically important morphological features are either present in all Ostariophysi or else they occur mosaically. All ostariophysans lack an ossified basisphenoid and all appear to have an orbitosphenoid. The saccular otolith (sagitta) is the smallest and either the utricular (asteriscus) or the lagenar (lapillus) is the largest. The pelvic fins are abdominal and rarely absent except in a few species or as an individual anomaly. There is often a single spinelike ray, rarely two, in the dorsal fin; this fin is absent from a few species. An adipose fin is often present, in some cases with a spine at its anterior border (Callichthyidae and Loricariidae) and in others with ossified rays (Mochokidae and a few Characidae). Frequently a dorsal cranial fontanelle is present, bordered either by the frontal or parietal, or by both. The skull is usually well ossified, with little cartilage in adults even of pygmy species. A mesocoracoid

is present in most representatives with a well-developed pectoral girdle. The jaws are protrusile in several groups, and in some instances they may have a reduced dentition or they may be completely edentulous. Pharyngeal teeth are highly specialized in several groups. Branchiostegal rays are few in number, usually five or fewer, but in certain catfishes there may be as many as 15. Scales are present or absent, usually cycloid, rarely ctenoid; in a few groups scales are replaced by bony plates. The head is usually without scales. The swim bladder is variously modified, but primitively it is divided into anterior and posterior chambers and it usually is physostomous. A suprapreopercular (an ossicle above the uppermost part of the preopercle and partially surrounding the preopercular canal) is present in many species. The caudal skeleton is variously reduced but primitively and commonly with all hypurals on one centrum. There is usually an epiphyseal bar between the frontals, and an epiphyseal branch of the cephalic sensory-canal system of the head passes over this bar. There is often a parietal branch of the cephalic sensory-canal system.

ORDER CYPRINIFORMES

Of the groups contained in the Cypriniformes, the characoids are the most primitive, and of these such forms as *Brycon* seem among the most generalized (Weitzman, 1962). However, Bertmar (1959, 1962) and Weitzman (1964) suggest that in some ways other characoids may be equally or more primitive. The matter needs considerably more investigation.

Each of the three suborders in the Cypriniformes has undergone an extensive evolutionary radiation. The basic trends and types of adaptation in these groups are best described separately. Nevertheless, it is possible to describe some basic characters and trends in the Cypriniformes that distinguish them from the Siluriformes. The Cypriniformes are less specialized than the Siluriformes despite the unusual modifications present in many species. In the Cypriniformes, parietal, symplectic, subopercular, and intermuscular bones are present. A quadrate-metapterygoid fenestra is present in primitive characoids, in most very specialized ones, but

in only a few cyprinoids (*Opsariichthys* and *Zacco*). When fusion between vertebrae occurs, the second and third vertebrae only are involved. In general, intervertebral fusion is rare. The fifth vertebra is the first to bear a fairly normal rib, and parapophyses usually are not fused to the centra. The body is usually scaled, rarely naked, and heavy bony plates are never developed. The largest otolith is usually the lagenar (asteriscus). Branchiostegal rays number three to five, and vomerine teeth are absent.

SUBORDER CHARACOIDEI: As noted above, the Characoidei are confined to Africa and the Neotropical Region north to the Rio Grande in North America. There are approximately 23 African genera with about 150 species, and 200 or more neotropical genera with between 900 and 1000 species.

We here recognize 16 families of characoids, all of which have been defined at the family-group level by previous authors (see Eigenmann, 1912; Regan, 1911a; Boulenger, 1904; and Weitzman, 1954, 1960c, 1962, and 1964). Characoids have been considered by many authors, for example, Eigenmann (1912) and Weitzman (1962), to belong to a single family, the Characidae. However, the amount of morphological divergence and the distinctness of many groups of characoids are compelling arguments for raising several to family rank.

Characoids have undergone a great amount of divergent evolution, but, despite their diversity of form, certain trends and patterns are discernible. Posttemporal fossae are present and are almost always well developed. A subtemporal fossa is usually poorly developed, and the species that have moderately developed fossae are never without jaw teeth. A rhinosphenoid is often present. The anterior margin of the vomer is invariably behind the ethmoid. A metapterygoid-quadrate foramen is present in most forms and is unquestionably primitive for the group. Teeth are usually present on the jaws and are of a variety of forms (they are absent from some families and reduced in others). Preethmoids (not the proethmoids of esocoids), and rostrals are absent. The pharyngeal bones and teeth are usually simple and opposing but may be quite specialized in some groups (for example, the Chilodontidae). The pal-

atines and pterygoid bones may be toothed. The premaxilla excludes the maxilla from the gape in only one or two specialized families (Weitzman, 1960b). An adipose fin is often present. The orbital bones are usually eight in number, and include an antorbital and a supraorbital, but the series may be reduced. The caudal skeleton consists of seven hypural elements that are connected to the ultimate centrum and its urostyle, and the principal fin-ray count is almost invariably 10/9. The Weberian apparatus is relatively simple in most cases, seldom involving intervertebral fusion, and the tripus is always attached to the third centrum by a bony lamella (Weitzman, 1962; Alexander, 1963).

SUBORDER GYMNOTOIDEI: The Gymnotoidei are peculiar, highly specialized, elongate, neotropical fishes unquestionably derived from characoid ancestors. No extensive research on their morphology and classification has been undertaken since that of Regan (1911a) and that of Ellis (1913). Anatomical investigations of gymnotoid interrelationships are needed. Géry and Vu-Tân-Tuê (1964) presented a key to the genera and families based largely on the work of Regan, Ellis, and Eigenmann and Allen (1942). Regan's analysis is still the most complete, and it forms the basis of the discussion presented here.

In recent years, interest in gymnotoids has centered on bioelectrogenesis and object-location in these fishes (Couceiro and de Almeida, 1961; Lissmann, 1961), specializations apparently shared with the unrelated mormyiform fishes. In addition to having electrogenic organs, these fishes possess several peculiar anatomical traits. They lack a rayed dorsal and pelvic fins. The caudal fin is absent or greatly reduced in size. The anal fin has an extremely long base, and it provides the primary means of locomotion. The basal pterygiophores of the anal fin are adapted uniquely to allow a circular motion of the lepidotrichia at their bases. Instead of having two or three sections (radials) to each pterygiophore, the gymnotoids have only one, and in these fishes each pterygiophore has a hemispherical cartilaginous head on its distal end which articulates directly with the lepidotrichium. This arrangement probably is diagnostic for the group; no char-

acid is known to show it (Weitzman, 1962). The vent is anterior, situated below the pectoral fins. The eyes are invariably small. The body may be compressed laterally or rounded.

Gymnotoids, in addition to the features mentioned above, have various other specializations, such as a restricted gill opening, the reduction or absence of certain bones (intercalar, palatine, pterygoid, mesocoracoid, and suboperculum), an elongate snout, and enlarged orbital bones. Despite these specializations, the relationship of the gymnotoids to the characoids is evident. The Weberian apparatus is simple and essentially like that of characoids. The skull is basically that of a characoid, especially in the otic region. In some species the swim bladder is enclosed in a bony case that differs from the type found in cyprinoids. One genus (*Gymnorhamphichthys*) has a ball-and-socket joint between the supraoccipital and the neural complex of the Weberian apparatus. Peculiar specializations in this group are many, and a complete study may alter the family arrangement accepted here.

SUBORDER CYPRINOIDEI: The Cyprinoidei are distributed throughout Africa, Eurasia, North America, and Middle America south to Guatemala. There are about 250 genera and 2500 species, of which the greater number occur in southern Asia—presumably their center of origin.

Despite Nichols' (1930 and 1943) opinions that the Catostomidae are the most primitive of the cyprinoids, and the probable ancestors of cyprinids, we agree with Ramaswami (1957) that such is highly unlikely. The catostomid skull has several characters that would exclude them from the ancestry of other cyprinoids. The generally simpler Weberian apparatus of cyprinids lacks certain catostomid specializations, as described by Nelson (1948). For us, this fact alone is enough to demonstrate the relatively primitive nature of the Cyprinidae. Moreover, the presence of a quadrate-metapterygoid fenestra in two cyprinids also suggests the primitive nature of these fishes (see below).

We look with hesitancy at some of the cyprinoid families proposed and discussed by Ramaswami (1948, 1952a, 1952b, 1952c, 1952d, 1953, 1955a, 1955b, 1957). For ex-

ample, the diphyletic origin for the Gastromyzonidae suggested by Ramaswami (1952d) seems questionable, and we also believe that the distinctions between the Gastromyzonidae and the Homalopteridae need further elucidation. The Cobitidae, Homalopteridae, and Gastromyzonidae appear related to one another and may be derived from some cyprinoid ancestor near the Cyprinidae. Ramaswami (1953) believed the Gastromyzonidae to be more closely related to the Cobitidae, and the Homalopteridae closer to the Cyprinidae. We await with keen interest Ramaswami's proposed and more complete discussion of the interrelationships of the cyprinoid families (Ramaswami, 1957, p. 302), but for the present we believe that the separation of homalopterids and gastromyzonids as separate families is not indicated. Nablant (1963) has made an interesting arrangement of the genera and subfamilies of the Cobitidae.

Cyprinoids as a group exhibit adaptive specializations not paralleled by those of any characoid. The lower pharyngeals have a reduced number of teeth, and the non-opposed upper pharyngeals are toothless. The former meet paired basioccipital processes that often unite below the aorta. The tripus of the Weberian apparatus is not attached to the centrum of the third vertebra by a bony lamella but is movably articulated with it. A metapterygoid-quadrate fenestra is almost universally absent. Subtemporal fossae are often well developed but are in some cases reduced; posttemporal fossae are variously developed but when present are not bridged by the epiotic as in the Characoidei. The preethmoid and median rostral bones are variously present or absent in accordance with the type of jaw movements. The jaws and palatine and pterygoid bones are toothless, and the premaxilla usually excludes the maxilla from the gape. Orbital bones are often reduced to simple tube bones or their number is greatly increased; they are characoid-like in the more primitive genera of the Cyprinidae. The Weberian apparatus is often modified, the most common modification being a fusion of the second and third centra. The swim bladder is often enclosed in a bony capsule in bottom-dwelling forms. The caudal skeleton is more variable than in the Characoidei, the

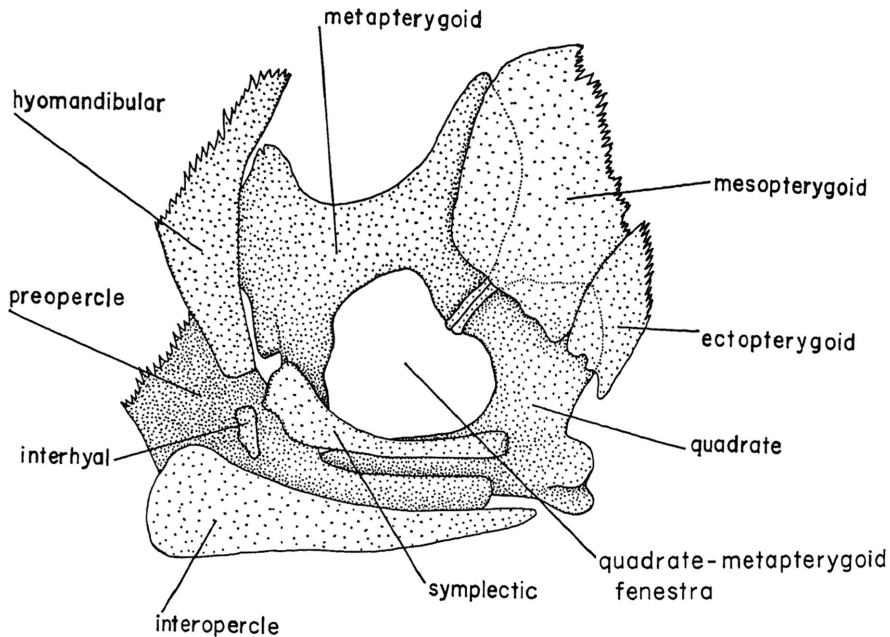


FIG. 9. Medial view of left side of part of jaw suspension of *Opsariichthys bidens*, anterior to right.

number of branched rays varying considerably (Gosline, 1961). There is no adipose fin except in some cobitids. Barbels are often present around the mouth. A frontoparietal fontanelle is present in some species, especially those of the Catostomidae.

Regan (1911a) and Ramaswami (1955a, 1955b) attempted to arrange the cyprinid genera in natural groups by sampling the osteology of one or two species of a few of the more than 200 nominal genera and subgenera. Both have admitted partial failure.

From the phyletic point of view, at least some characters appear to have significance at the subfamily level in cyprinids, e.g., the presence or absence of a quadrate-metapterygoid fenestra (see fig. 9). This foramen is common in characoids (see Regan, 1911a, and Weitzman, 1962, for figures), and from this it may be assumed that its presence is primitive for cyprinids and, indeed, all cyprinoids. Regan (1911a) reported it only for *Opsariichthys* among the cyprinids, but we found it also in the closely related *Zacco*. We did not find it in several samples of *Tanichthys*, *Rasbora*, *Danio* (or *Brachydanio*), *Barilius*, *Aphyocypris* (or *Nicholsicypris*),

Hemigrammocypripis, *Notropis*, *Carassius*, *Cyprinus*, *Hesperoleucus*, *Barbus* (*Puntius*), or *Sarcocheilichthys*.

Fusion of the centra of the second and third vertebrae seems to be an important and specialized character of the Weberian apparatus, although it may have occurred independently several times in cyprinids. The character must be carefully evaluated when groups of these fishes are defined morphologically. The absence of this fusion represents perhaps a somewhat primitive condition; and its presence, a specialization. Since *Barilius*, as represented by *B. ubangensis* and *B. pulchellus*, has neither separate second and third vertebral centra nor a quadrate-metapterygoid foramen, we question the conservative nature of *Barilius* proposed by Regan (1911a) and Brittan (1954).

Cyprinids, for example, *Esomus*, with a laterosensory canal in the sphenotic are specialized, at least in this respect (see Ramaswami, 1955b). Most cyprinids and characids lack such a canal. This character should be investigated in the genera thought to be relatives of *Esomus*. The ontogeny of the sphenotic and separate "dermosphenotic"

(uppermost posterior infraorbital bone) should be investigated thoroughly in *Esomus*.

Perusal of the work of Ramaswami (1955a, 1955b) and Regan (1911a) reveals several other characters of possible significance at the subfamily, tribal, or generic level. Caution, however, must be used. For example, Ramaswami (1955b) noted the absence of preethmoids in *Esomus*, *Leuciscus*, *Phoxinus*, *Scardinus*, *Aristichthys*, and *Notropis*, among others. In each of the genera mentioned he examined only one species, but in his conclusions he considered those genera to be without the preethmoid. Ramaswami (*loc. cit.*) noted the absence of the preethmoid in *Notropis cornutus*. Harrington (1955) showed it to be present in *Notropis bifrenatus*, and we have found it in *Notropis cocco-genis*, *Notropis galacturus*, and *Notropis lutrensis*. We have found preethmoids in *Notropus c. cornutus*, but have not re-examined Ramaswami's specimens. Possibly his specimens lacked preethmoids, since they are only slightly ossified in the adult individuals at hand. Although the presence or absence of this endochondral ethmoid ossification may be of some phylogenetic significance, it should be studied in closely related species and in specimens of different sizes before generalizations about its presence or absence in genera can be made.

ORDER SILURIFORMES

This is an unusually well-defined order of fishes. A majority of its approximately 30 families and perhaps 2000 species are found in South America or Africa, and most are confined to fresh water. However, the Ariidae are widely distributed in tropical and subtropical marine coastal areas, and the Plotosidae are mainly from the Indo-Pacific. A few families are found in the temperate Eurasian Region and one, Ictaluridae, is dominant in North America. The most primitive of living catfish families, the Diplomystidae, is a relic confined to southern South America. This family not only has teeth on the maxilla, but it has a relatively primitive Weberian apparatus, for a siluriform (Eigenmann, 1927).

The interrelationships of the fishes of this order are poorly known. It is certain that the Diplomystidae are primitive and also that

the Nematogenyinae in the Pygidiidae appear to have a simple Weberian apparatus and may be relatively primitive, at least for that family. We cannot accept the theory of Hoedeman (1954, and *in litt.*) that the Loricariidae are the most primitive of living catfishes and near the ancestral "stem" of the Ostariophysi. It does appear that the Loricariidae, the Callichthyidae, and possibly the Pygidiidae and a few other families may represent one or more distinct lines of evolution within the catfishes. The Ariidae are often considered relatively primitive, but their lack of a mesocoracoid and fairly complex Weberian apparatus casts considerable doubt on this idea. Indeed, the Weberian apparatus of the related families Bagridae, Ictaluridae, and Pimelodidae appears somewhat more primitive than that of the Ariidae. Tilak (1963a, 1963b, 1963c, 1965) also has cast serious doubt on the primitive nature of the Ariidae. Despite numerous recent papers (see summary at end of this section) on the morphology of catfishes, no satisfactory arrangement of families is at present possible.

The Siluriformes may be described as Ostariophysi without a parietal, symplectic, suboperculum, first and second pharyngobranchials, and epipleural and epineural bones. True scales are absent, and the body is naked or covered with bony plates. Small spinules or prickles may be present in the skin of some species. Short tubular ossicles enclose the lateral line in some species. The second, third, and fourth vertebrae of the Weberian apparatus are fused to a single ossification called a "complex vertebra." Additional posterior vertebral centra are frequently fused to or united by exceedingly tight joints with the complex vertebra. The tripus is suspended from this complex by a bony lamella somewhat similar to that in characoids. A small, platelike posttemporal (when present) overlies the joint between the pterotic and epiotic and reaches the supraoccipital medially. The supracleithrum is complicated and articulated with the posttemporal, epiotic, and often with the pterotic. Frequently, a ventral process of the supracleithrum (ossified transscapular ligament) meets the basioccipital. The lower part of the supracleithrum is deeply forked for the reception of the upper limb of the cleithrum. A

mesocoracoid is usually present but is absent from some families. The first pectoral and dorsal fin rays often are complicated, hard, pungent spines which frequently bear spinules, serrations, pungent spinelets, or barbs.

As noted by Regan (1911b; see also Starks, 1930, and Tilak, 1963a), the pectoral girdle is characteristic of the group, the spine having at its base a "friction lock" with the coracoid bone. Tilak (1963a) noted a general tendency in several catfish families for the mesocoracoid to fuse to the coracoid, and Starks (1930) stated that the coracoid, mesocoracoid, and scapula fuse to form a complex bone. The dorsal spine also often has a characteristic locking device, with a "locking element," possibly a modified first spine, between the anteriorly placed basal predorsal plate and the anterior base of the spine itself.

An adipose fin is usually present in catfishes. It is in some cases preceded by a spine and rarely contains fin rays. The swim bladder, when well developed, is divided into anterior and posterior segments by a partition, not a constriction as in most characoids and cyprinoids. Barbels are often present and elongate, much more so than in the cyprinoids, also they frequently occur on the lower jaw. The caudal skeleton of catfishes is variously developed, the number of principal rays differing considerably. Pterygoid and palatine bones are frequently toothed as is the vomer. The premaxilla and the dentary are often toothed, but the maxilla is reduced in size, almost invariably toothless, and forms the base of a barbel.

Works on the morphology of catfishes are numerous and of widely varying quality, making an assessment of these and of the evolution of catfishes very difficult. A great deal of morphological work still needs to be done, especially in the South American families. Two of the more important works on catfish osteology and other morphology not mentioned above are the classics of Bridge and Haddon (1893) and Chranilov (1929). Other works are: McMurrich (1884), Wright (1884, 1885), Kindred (1919), Reichel (1927), David (1935), Sheldon (1937), Nair (1938), Merriam (1940), Eaton (1948), Bamford (1948), Krandikar and Masurekar (1954), Nawar (1954), Jayaram (1955), Srinivasachar (1957,

1958, 1959), Joseph (1960), Masurekar (1962), and Tilak (1964). This list is in no sense complete, but, with the other works cited, should serve to introduce the student to the literature of catfish morphology and evolution.

SUPERORDER PARACANTHOPTERYGII

The fishes grouped together in this superorder represent a spiny-finned radiation more or less comparable morphologically with that of the Acanthopterygii. So close are the parallels between the generalized and the advanced members of the Paracanthopterygii and Acanthopterygi that the representatives of these two groups have not previously been separated. At times, however, many of the paracanthopterygians have been grouped together as *Pediculati* or *Jugulares*. It is historically interesting that one of the orders regarded by us as most primitive, the *Batrachoidiformes*, often has been treated as an advanced and very specialized derivative of typical acanthopterygian stock. The first of the toadfishes to be discovered was described prophetically by Linnaeus as *Gadus tau*.

The argument favoring the creation of this superorder is as follows: If the lophiiforms and gobiesociforms are related to the batrachoidiforms, as we have reason to believe they may be, and if the batrachoidiforms are the descendants of an ancient pre-acanthopterygian radiation that produced also the percopsiforms and gadiforms, then the fishes here assembled evidently represent a distinct lineage that must be remote from acanthopterygian history.

No acanthopterygian, not even the most primitive, is known to possess a caudal skeleton comparable with that of the generalized paracanthopterygians, nor is it conceivable to us how a perchlike fish could have reacquired a pre-perciform type of cervical and caudal vertebra, and one pectoral radial (to mention but three features), to produce the characteristic batrachoidiform facies. It is everywhere evident that the trend of the spiny-finned fishes has been toward reduction, and we view it as improbable that whole groups of fishes reassumed protacanthopterygian-like features of the vertebrae, jaw muscles, pectoral girdle, caudal skeleton, and fin

rays from a perchlike ancestor. One of the earliest known perciforms, *Prolates* from the Lower Paleocene of the Paris Basin, has been examined by us, and we are convinced that this fish had already attained a level of specialization that would exclude it from the ancestry of anything save other perciforms.

It may be argued that the more primitive Beryciformes of the Acanthopterygii could have given rise to the paracanthopterygian groups. The objections to such a possibility are many, for example, the fact that the living *and* fossil beryciforms have, in common with generalized perciforms but with no gadiform or percopsiform, the development of a subocular shelf on the infraorbital bones, the division of the hypurals into six or seven elements and their distribution usually on a terminal half-centrum, the displacement of Baudelot's ligament onto the basicranium by fusion of the first vertebra to the basioccipital, and the failure to develop or absence of a mm. levator maxillae superioris series and the great development of the superficial division (A_1) of the m. adductor mandibulae in the jaw mechanism. Another objection to alignment of beryciforms with primitive paracanthopterygians is the demonstrably direct relationships between the known fossil, and some living, beryciforms and the perciforms (Patterson, 1964). Patterson (personal communication) knows of no evidence in the fossil material that even hints at a relationship between the Beryciformes and any group included here in the Paracanthopterygii. Moreover, Freihofer (1963) has not found patterns of the recurrent facial nerve in any paracanthopterygian that closely resemble those of perciforms. Lastly, it is evident to us, as detailed below, that the Batrachoidiformes are more primitive than any beryciform. One might almost look upon them, together with the percopsiforms (*sensu lato*), as the descendants of a sort of "paraberycoid" radiation that gave some of its main characteristics to the more specialized lophiiforms and gobiociforms on the one hand and to the gadiforms on the other. The essential feature of the Paracanthopterygii, however, is that each group, even the most advanced, contains one or more members that by current criteria are more primitive than any known member of the Acantho-

pterygii. The Paracanthopterygii have clearly trended toward the acanthopterygian form, and some species quite evidently have attained that level of organization. Because no one group is without representatives having pre-acanthopterygian features, they are at once excluded from the acanthopterygian assemblage, and the phylogenetic integrity of this superorder is emphasized thereby. Since paracanthopterygians have some features that seemingly had their origin at a pre-acanthopterygian level, the question may be raised whether the hypothetical "paraberycoids" and the berycoids were two distinct and quite independent radiations from the salmoniform level, as suggested above. The various advanced salmoniforms (such as the Myctophoidae) possess in the aggregate all the necessary specializations on which to build each of these two basic types of spiny-finned fishes (see discussion under Protacanthopterygii).

The more primitive paracanthopterygian orders (Percopsiformes, Gadiformes, Batrachoidiformes) are united by the following features, present in most or all species of these groups, which also set them apart from the acanthopterygian stem: mm. levator maxillae superioris present and well developed (pls. 21, 22); m. adductor mandibulae superficialis (A_1) markedly reduced or absent; infraorbital bones, when present, without a subocular shelf; Baudelot's ligament from the posteroventral edge of supracleithrum to first vertebra; caudal skeleton consisting of three hypurals only, the lowermost strutlike, the second broadly triangular and attached to a penultimate centrum, the third hypural also broadly triangular but attached to the terminal half-centrum.

Regan (1912a) had appreciated many of these characteristics in his comments on a probable relationship of the batrachoidiforms with the lophiiforms. He combined both groups as suborders of an order Pediculati and he wrote: "The Batrachoidea are here included in the Pediculati rather than in the Percomorphi, for it can hardly be the case that the resemblances in osteologic characters, especially in the structure of the pectoral arch, are not due to real affinity. In many ways the Batrachoids are more generalized than the typical Pediculates, but in

some respects, notably the reduction in number of the pelvic fin-rays and the ankylosis of parietal and epiotic, they are more specialized. The Pediculates might certainly be regarded as highly specialized percoids, were it not that in the Percomorphi all the principal hypurals are attached to the last vertebra, whereas in the Batrachoids the upper hypural plate is ankylosed to the last half-centrum, and that supporting the lower half of the fin is united to the preceding centrum, much as in the Salmopercae [= Percopsiformes, in part]; this seems to be a primitive character."

The clingfishes resemble toadfishes in many superficial traits, and the possible relationship of these two groups has been remarked on by Starks (1905): "The families Batrachididae and Callionymidae offer some slight indications of relationship to the Gobiocidae, and the weight of evidence is thrown towards the former family by the young of some or all of them having a ventral sucking disc just behind the base of the pectorals. The family Batrachididae further resembles the Gobiocidae in having the suborbital ring reduced to a small preorbital bone, only very small parapophyses present posteriorly, no myodome, and a single superior pharyngeal present on each side. As opposing the idea of relationship the Batrachididae have five long actinosts, the posttemporal forms an integral part of the cranium, the palatine is normally joined to the pterygoid, and the mesopterygoid, metapterygoid, alisphenoid, and basi-branchials are present."

In at least some ophidioids the parietals are much enlarged and meet at the midline over the supraoccipital. The condition is illustrated by Emery (1880) in *Carapus*. It occurs also among gadids, for example, in species of *Merluccius*, and it is closely approached in a number of others, including *Raniceps* and *Odontogadus* (see Svetovidov, 1948). More recently it has been reported by Leray (1961) in the gobiocid *Gouania*.

The position of the ophidioid fishes among the gadiforms was suggested by Rosen (1962) on the basis of similarities in their jaw mechanisms, habits, and in general body form. Their proposed relationship to the Gadiformes is supported also by the trend in both groups for the parietals to enlarge medially

(actually meeting in the midline in some ophidioids), and by the discovery of a dual-centrum caudal skeleton in the brotulid *Ogilbia* which is precisely like that of gadoids. Both gadoids and ophidioids tend to develop complex swim bladders that are functionally related to the pleural ribs and parapophyses, and Freihofer (1963) has interpreted the ophidioid pattern of the recurrent facial nerve as similar to that of gadiforms. The ophidioids differ from gadiforms in having the first vertebra fused to the skull, hence in having Baudelot's ligament to the basicranium (for example, in *Genypterus blacodes*, *Brotula multibarbata*, and *Neobythites steaticus*). However, in many ways they are no more different from gadoids than are the macrouroids, and we prefer to group them all together in a single order.

Freihofer (1963) also pointed to the great similarity of the pattern of the recurrent facial nerve in ophidioids and zoarcids. That zoarcids are members of the gadiform complex is suggested also by the tendency of their parietals to be enlarged and to meet in the midline (e.g., in *Neozoarces*, according to Makushok, 1961), for Baudelot's ligament to join the base of the first vertebra instead of the basicranium (e.g., in *Lycodes* and *Macrozoarces*), and for the pleural ribs to be poorly developed. In common with many gadiforms, the zoarcids are elongate, tailless, soft-bodied fishes of the deeper waters.

The inclusion of the zoarcids as a suborder in the Gadiformes raises the question of the relationships of other fishes formerly grouped in the Blennioidei of the Perciformes, such as the also elongate and soft-bodied anarhichids and congrogadids. Indeed it seems to us that a thorough review of the blennioids, trachinoids, uranoscopoids, and notothenioids, and perhaps even the gobioids, is needed before the limits of the Paracanthopterygii and Acanthopterygii can be defined sharply. The relationships of one or more of those five groups to the toadfishes, codfishes, cusk eels, or lophiiforms were suggested or implied in the earlier anatomies or classifications of Günther (1862), Gill (1872, 1884), Emery (1880), Jordan and Evermann (1898), Boulenger (1901, 1904), Regan (1903, 1912a, 1912b), Starks (1905, 1923), Jordan (1905), Gregory (1907), Goodrich (1909), and Allis

(1909), and more recently in the work of Svetovidov (1948, fig. 3; 1961), Rosen (1962), and Freihofner (1963).

SUPERORDER ATHERINOMORPHA

The anatomical and developmental characteristics of the Atheriniformes, the only contained order of the Atherinomorpha, were given by Rosen (1964). In that paper the nearest relatives of the atherinomorphs were presumed to be among the ancestors of the Acanthopterygii. The amblyopsid fishes (Percopsiformes, in part) were long associated with certain atheriniforms. We oppose that alignment and include the Amblyopsidae in the most primitive surviving group of the Paracanthopterygii.

SUPERORDER ACANTHOPTERYGII

The classification of the Beryciformes presented here includes all but one group (the Cretaceous Dinopterygoidei of Patterson, 1964) of similar subperciform fishes that are generally considered to be antecedent to the Perciformes. The dinopterygoids are omitted from this classification simply because we have not included exclusively fossil groups. However, we are fully aware that from the standpoint of an enduring arrangement of the Acanthopterygii, the Dinopterygoidei must be given special consideration. The reasons were a subject of Patterson's (1964) recent major review of the Mesozoic acanthopterygians of the English Chalk. In that paper, Patterson suggested that the Lampridiformes and such perciform groups as the Menidae, Carangidae, Acanthuroidei, Balistoidei, Chaetodontidae, and Centrarchidae might be derived from the dinopterygoid stem, and that the Serranidae, Scorpididae, and others might have arisen from a polymixioid line. The Berycoidei apparently were not implicated in the origin of any modern perciform group, nor were they particularly closely related to the polymixioids and dinopterygoids.

Although some of Patterson's evidence for a direct relationship between fossil beryciform groups and modern perciform ones is equivocal, as he himself admits, other evidence of his is unequivocal in its indications of polyphyly among the perchlike fishes. It is incontestably clear, for example, that scor-

pidids, monodactylids, and kyphosids are among the most primitive perciforms (and in some ways more primitive than serranids) because they possess, in common with beryciforms, ectopterygoid and entopterygoid teeth and a separate foramen for the hyomandibular trunk of the facial nerve in the wall of the pars jugularis. These perciform families bear a strong resemblance to the polymixioids *Omosoma* and *Berycopsis* and share with *Berycopsis* sessile ribs and scales on the bases of the median fins. Of the polymixioids, indeed of all beryciforms, there is a single form known, the Upper Cretaceous (Senonian) *Sphenocephalus*, that is generalized enough to have given rise to the serranid-percid line. On the other hand various groups of specialized dinopterygoids show extensive similarities to various specialized perciform families. For example, the aipichthyids resemble carangids in having a deep trunk, long dorsal and anal fins with few spines and with the anterior soft rays elongate, a high supraoccipital crest arising over the orbit, no ornamentation on the head bones, upturned mouth, an elongate supramaxilla, cycloid scales, a deeply forked caudal fin, and similarities in vertebral number, form of cleithrum and coracoid, and in the character of the interhemal and interneural radials. So close are the aipichthyids to carangids that *Aipichthys* had been treated as a perciform near or actually in the Carangidae, but the genus must be included with the beryciforms because of the presence of an orbitosphenoid, eight branchiostegals, epineural bones, and 17 branched caudal rays.

The resemblances of other dinopterygoid families to chaetodontids, centrarchids, acanthuroids, and balistoids are less impressive, but the evidence is clear. To quote Patterson: " . . . is evidence that the resemblances between the various beryciform and perciform groups indicate real relationship, for if the resemblances were due to convergence, one would expect there to be as many characters in which the beryciform genera are more specialized than the percoid groups as there are characters in which the percoid groups are more specialized than the Beryciformes." Patterson goes on to remark that if " . . . it is accepted that at least some of these different Beryciformes are near the ancestry of the different perciform groups which

they resemble, we have a new picture of the origin and evolution of the Perciformes."

Patterson noted that "This type of evolution, a major group evolving polyphyletically by the loss or development of characters independently and more or less contemporaneously in several different lines, is apparently rather common in the history of the vertebrates . . ." and he added ". . . that the great majority of the changes which have taken place in the evolution of acanthopterygians can be accounted for by functional trends. But the three main characters which separate the Beryciformes from the Perciformes, the presence or absence of an orbitosphenoid and the number of pelvic and caudal fin-rays, cannot be accounted for in terms of function. These three characters must have changed independently and uniformly in each of the lines of Perciformes, yet the characters are apparently nonadaptive."

Because of the strong indications of a polyphyletic origin of the Perciformes raised by Patterson's work, it is evident that future natural classifications of these fishes may be fundamentally unlike the conventional arrangement used here. We can imagine either a system in which all groups of beryciforms and perciforms are united in a single order, or one in which two to several new orders are established each of which would include a series of basal beryciforms and the derived perciform types. In no case can we envision a long, happy future for the orders Beryciformes and Perciformes as they now stand, a point that has already been sufficiently emphasized by our establishment of the Paracanthopterygii (see discussion above).

Classification within the very large order Perciformes is not in a good state at the time we write, although a number of workers are actively investigating either the whole group (e.g., Freihofer, 1963, and in progress) or parts of it (e.g., Liem, 1963, the anabantoids; Smith, 1965, and in progress, the percoids; Haedrich, work in progress on stromateoids; Böhlke, 1960, the percoids with a disjunct lateral line; Robins and De Sylva, work in progress on scombroids; Victor Springer, in preparation, on blennies; and others). In addition there is a great deal of past work, especially on different organ systems, which contains material useful for perciform classifica-

tion (many references of general import are given in the bibliographies of Rosen, 1962 and 1964).

Because of the absence at present of an over-all synthetic treatment, the subordinal and familial classification of the Perciformes given below is highly tentative and subject to extensive revision, although a great many of our colleagues have given us help in regard to the whole or parts of it. Apart from the problem of the central acanthopterygians, the composition and relationships of the Gasterosteiformes, Zeiformes, Synbranchiformes, Channiformes, and Tetraodontiformes have still to be assessed. More than one of these extra-perciform groups is suspected of being polyphyletic.

The scorpaeniform fishes represent a more or less typical example of the work that needs still to be done. Many of these species are similar to cods in the formation of the parietals and in some respects of the cheek muscles and to the toadfishes in body form and in the presence of a valved, horseshoe-shaped swim bladder with extrinsic drumming muscles. Others are clearly of acanthopterygian affinities, and those species most like the perciforms appear also to be the most generalized ones in the order. Although most scorpaeniforms lack a subocular shelf on their well-developed infraorbital bones, such perchlike forms as *Sebastes* and *Sebastodes* do have a well-developed shelf, approximately 24 vertebrae, fewer than eight branchiostegals, a pelvic fin consisting of a spine and five soft rays, three anal spines, and principal caudal fin rays that never exceed 17 in number. Nevertheless, the relationships of the Scorpaeniformes to the perciforms is not well established. Freihofer (1963), for example, has divided the scorpaeniforms into three well-marked groups on the basis of the form and orientation of the recurrent facial nerve. The distinctive pattern in scorpaenids could have been derived from a widespread perciform pattern that typifies most species of the Serranidae. The pattern in hexagrammids, cottids, and cyclopterids could have been derived from one characteristic only of *Roccus* and its near allies, although the hexagrammid-cottid-cyclopterid system of the recurrent facial is most like that of gobioides. The recurrent facial of the Anoplopomatidae,

however, is tentatively regarded as being closest to that of the gadoid fishes. On the basis of osteological and other evidence, Quast (1965) also concluded that the Scorpaeniformes are complex. He wrote: "The mail-cheeked fishes may be an artificial assemblage containing at least three distinct evolutionary lines, scorpaenid, anoplomatid, and hexagrammid-cottid." The present writers have found that at least the representatives of the hexagrammid-cottid line have a pattern of cheek muscles that seemingly could have been derived as easily from the batrachoidid as from the percoid type (pl. 23). We have also determined that various scorpaenids (e.g., *Scorpaena cirrhosa*, *S. scrofa*, *Pontinus kuhlii*, and *Centropogon robustus*) possess modified epipleural ribs that extend between the upper shoulder girdle and the neural arch of the first vertebra as does the so-called endocleithrum of batrachoidids.¹ Moreover, in *Pontinus kuhlii* and *Centropogon robustus*

Baudelot's ligament extends to the base of the first vertebra (not to the basicranium as in perciforms and some, if not all, living beryciforms). Despite the suggestions that the scorpaeniforms are polyphyletic, all species of each line that we have examined have the same highly distinctive type of caudal skeleton in which two platelike hypurals are sutured to the terminal half-centrum. The particular characters of their caudal skeleton are not duplicated in the species of any other acanthopterygian line that we have studied. For the present, therefore, we retain these fishes as a distinct order and align them tentatively with the Acanthopterygii.

¹ Starks (1923) claimed that the "endocleithrum" is not a modified rib, but the ossified Baudelot's ligament. We doubt this interpretation because that bone is incorrectly oriented to be the suspensory ligament and because a normal Baudelot's ligament is invariably present in toadfishes in addition to the "endocleithrum." We are content to regard it as a modified epipleural rib.

PROVISIONAL OUTLINE CLASSIFICATION OF THE TELEOSTEAN FISHES¹

DIVISION I

SUPERORDER ELOPOMORPHA

Order Elopiformes (Isospondyli in part, Clupeiformes in part)

Suborder Elopoidei

Elopidae (Elopsidae in part)

Megalopidae (Elopsidae in part)

Suborder Albuloidei

Albulidae (including Pterothrissidae, Bathythrissidae)

Order Anguilliformes (Apodes, Lyomeri, Saccopharyngiformes, Monognathiformes, Anguillomorphi)

Suborder Anguilloidei

Anguillidae

Moringuidae (including Stilbiscidae, Anguillichthyidae, Ratabouridae)

Myrocongridae

Xenococongridae (including Chlopsidae, Echelidae in part, Myridae in part, Muraenichthyidae,

Chilorhinidae)

Muraenidae (including Echidnidae, Heteromyridae)

Heterenchelyidae (Heterenchelidae)

Dysomminidae (Dysominidae)

Muraenesocidae (including Sauromuraenesocidae)

Neenchelyidae

Nettastomatidae (Nettastomidae)

Nessorhamphidae

Congridae (Congeridae, Leptocephalidae, including Heterocongridae, Colocongridae)

Ophichthidae (Ophichthyidae, including Myrophidae, Echelidae in part, Myridae in part)

Todaridae

Synaphobranchidae (including Ilyophidae)

Simenchelyidae (Simenchelidae)

Dysommidae

Derichthyidae

Macrocephenchelyidae (Macrocephenchelidae)

Serrivomeridae (including Gavialicipitidae)

Nemichthyidae (including Avocettinidae, Avocettinopsidae)

Cyemidae

Aoteidae (Aoteridae)

Suborder Saccopharyngoidei

Saccopharyngidae

Eurypharyngidae

Monognathidae

Order Notacanthiformes (Lyopomi, Heteromi, Halosauriformes)

Halosauridae

¹ Our attention has been called to a recent purportedly complete list of the generic and familial names of fishes (Golvan, 1962). Its author does not admit to familiarity with Jordan's "Classification" (1923), and the errors in it are exceedingly numerous. In addition, a curious and little-known classification was published by E. Le Danois in 1943. Although this author's three major groups (orders) of teleosts are manifestly polyphyletic, his alignment of their contained suborders departs from those of Regan and Berg (Berg's classification was, apparently, not seen by Le Danois). We can find little to support the reasoning behind the construction of most of the proposed groups. The principal weakness of this classification lies in the author's failure to consider

more than a few, generally superficial and insufficiently studied characters, combined with rather naive views on the interpretation of palaeontological evidence. Two other recent classifications, both in Japanese, which depart radically from each other and from our own, were proposed by Matsubara (1955, 1963). In these, the author follows the Stenzel system of ordinal suffixes, but his ordinal names are not incorporated in our present classification. Finally, we must mention a classification proposed by Tretiakov (1944), which is the outline of an arrangement of the orders and suborders based largely on the pattern of cephalic lateral-line canals. A number of new ordinal names were proposed which are accorded a place in our lists of synonyms.

Lipogenyidae (Lipogenidae)
 Notacanthidae

SUPERORDER CLUPEOMORPHA

Order Clupeiformes (Isospondyli in part)

Suborder Denticipitoidei

Denticipitidae (Igborichthyidae)

Suborder Clupeoidei

Clupeidae (Clupidae, including Dorosomatidae, Dorosomidae, Clupanodontidae, Dussumieridae, Dussumieriidae, Dussumeriidae, Congothrissidae, Pristigasteridae)

Engraulidae (Engraulididae, including Stolephoridae)

Chirocentridae

DIVISION II

SUPERORDER OSTEOGLOSSOMORPHA

Order Osteoglossiformes (Isospondyli in part, Clupeiformes in part)

Suborder Osteoglossoidei

Osteoglossidae (including Arapaimidae, Clupisudidae, Heterotidae)

Pantodontidae

Suborder Notopteroidei

Hiodontidae (Hyodontidae)

Notopteridae

Order Mormyriiformes (Isopondyli in part, Clupeiformes in part, Scyphophori)

Mormyridae

Gymnarchidae

DIVISION III

SUPERORDER PROTACANTHOPTERYGII

Order Salmoniformes (Isospondyli in part, Clupeiformes in part, Galaxiiformes, Haplomi, Xenomi, Iniomi, Scopeliformes, Myctophiformes)

Suborder Salmonoidei

Salmonidae (including Coregonidae, Thymallidae)

Plecoglossidae

Osmeridae

Suborder Argentinoidei

Argentinidae (including Xenophthalmichthyidae)

Bathylagidae (including Microstomatidae, Microstomidae)

Opisthoproctidae (including Dolichopterygidae, Macropinnidae, Winteridae, Winteriidae)

Suborder Galaxioidei

Salangidae

Retropinnidae

Galaxiidae (Galaxidae, including Paragalaxiidae)

Aplochitonidae (Haplochitonidae, including Prototroctidae)

Suborder Esocoidei

Esocidae (Luciidae)

Umbridae (including Dalliidae, Novumbridae)

Suborder Stomiatoidi

Gonostomatidae (Gonostomidae, including Maurolicidae)

Sternoptychidae (Sternoptychiidae)

Astronesthidae

Melanostomiidae

Malacosteidae

Chauliodontidae (Chauliodidae)

Stomiatidae

Idiacanthidae (including Stylophthalmidae, Stylophthalmoidae)

Suborder Alepocephaloidei

Alepocephalidae (including Platytroctidae, Platyproctidae, Searsidae, Searsidae)

Suborder Bathylaconoidei

Bathylaconidae

Suborder Myctophoidi

- Aulopodidae (Aulopidae)
- Synodontidae (Sauridae, Synodidae, Bathysauridae)
- Harpadontidae (Harpodontidae)
- Chlorophthalmidae
- Bathypteroidae (Bathypteridae, Benthosauridae)
- Ipnopidae
- Paralepididae (Paralepidae, including Sudidae)
- Omosudidae
- Alepisauridae (Alepidosauridae, Plagyodontidae)
- Anopteridae
- Evermannellidae (Odontostomidae)
- Scopelarchidae
- Scopelosauridae (Notosudidae)
- Myctophidae (Scopelidae)
- Neoscopelidae

Order Cetomimiformes (Isospondyli in part, Clupeiformes in part, Stephanoberyciformes in part, Scopeliformes in part, Ateleopiformes, Chondrobrachii, Giganturiformes)

Suborder Cetomimoidei

- Cetomimidae
- Barbourisiidae (Barbourisidae)
- Rondeletiidae

Suborder Ateleopodoidei

- Ateleopodidae (Ateleopidae, Podatelidae)

Suborder Mirapinnatoidei

- Kasidoridae (Kasidoroidae)
- Mirapinnidae (Mirapinnatidae)
- Eutaeniophoridae (Taeniophoridae)

Suborder Giganturoidei

- Giganturidae
- Rosauridae (?based on young of giganturid)

Order Ctenothrissiformes

- Macristiidae

Order Gonorynchiformes (Isospondyli in part, Clupeiformes in part, Chanoiformes)

Suborder Gonorynchoidei

- Gonorynchidae (Gonorhynchidae)

Suborder Chanoidei

- Chanidae (Chanoidae)
- Kneriidae (including Cromeriidae, Grasseichthyidae)
- Phractolaemidae

SUPERORDER OSTARIOPHYSI

Order Cypriniformes (Plectospondyli in part, Heterognathi, Gymnonoti, Glanencheli, Eventognathi)

Suborder Characoidei

- Characidae (Characinidae, including Crenuchidae, Acestrorhynchidae, Serrasalminidae, Tetragonopteridae, Creagrutidae, Glandulocaudidae)
- Erythrinidae
- Ctenoluciidae (Xiphostomidae, Xiphostomatidae, including Hepsetidae in part)
- Hepsetidae
- Cynodontidae
- Lebiasinidae (including Nannostomidae)
- Parodontidae
- Gasteropelecidae (Gastropelecidae)
- Prochilodontidae
- Curimatidae (including Anodontidae)
- Anostomidae
- Hemiodontidae (Hemiodidae, including Bivibranchiidae)
- Chilodontidae
- Distichodontidae

- Citharinidae
- Ichthyboridae (Ichthyoboridae)
- Suborder Gymnotoidei
 - Gymnotidae
 - Electrophoridae
 - Apteronotidae (including Sternarchidae, Sternopygidae)
 - Rhamphichthyidae
- Suborder Cyprinoidei
 - Cyprinidae (including Gobiobotidae, Medidae)
 - Gyrinocheilidae
 - Psilorhynchidae
 - Catostomidae
 - Homalopteridae (including Gastromyzonidae, Gastromyzontidae, Lepidoglanidae)
 - Cobitidae (Acanthopsidae, including Adiposidae)
- Order Siluriformes (Plectospondyli in part, Cypriniformes in part, Nematognathi, Siluroidiformes)
 - Diplomystidae
 - Ictaluridae (Amiuridae, Ameiuridae)
 - Bagridae (including Porcidae, Mystidae)
 - Cranoglanididae
 - Siluridae
 - Schilbeidae
 - Pangasiidae
 - Amblycipitidae (Amblycepidae)
 - Amphiliidae
 - Akysidae
 - Sisoridae (Bagariidae)
 - Clariidae
 - Heteropneustidae (Saccobranchidae)
 - Chacidae
 - Olyridae
 - Malapteruridae (Malopteruridae, Torpedinidae, not an electric ray)
 - Mochokidae (Synodidae, Mochockidae, Mochochidae, Mochocidae)
 - Ariidae (Tachysuridae, Bagreidae, including Doiichthyidae)
 - Doradidae
 - Auchenipteridae (including Trachycorystidae)
 - Aspredinidae (Bunocephalidae)
 - Plotosidae
 - Pimelodidae (including Pseudopimelodidae, Callophysidae)
 - Ageneiosidae
 - Hypophthalmidae
 - Helogeneidae (Hologenidae)
 - Cetopsidae
 - Trichomycteridae (Pygidiidae)
 - Callichthyidae
 - Loricariidae (including Hypostomidae)
 - Astroblepidae (Argidae, Cyclopiidae, Cyclopidae)
- SUPERORDER PARACANTHOPTERYGII
 - Order Percopsiformes (Microcyprini in part, Cyprinodontes in part, Cyprinodontiformes in part, Amblyopsiformes, Salmopercae, Xenarchi, Percopsomorphi)
 - Suborder Amblyopsoidei
 - Amblyopsidae (Hypsocidae, Hypsaeidae)
 - Suborder Aphredoderoidei
 - Aphredoderidae
 - Suborder Percopsoidei
 - Percopsidae
 - Order Batrachoidiformes (Jugulares in part, Haplodoci, Perciformes in part, Pediculati in part)
 - Batrachoididae (Batrachidae)

- Order Gobiesociformes (Xenopterygii, Gobiesocomorphi, Perciformes in part)
 - Gobiesocidae (including Diademichthyidae)
- Order Lophiiformes (Pediculati in part)
 - Suborder Lophioidei
 - Lophiidae
 - Suborder Antennarioidei
 - Brachionichthyidae
 - Antennariidae
 - Chaunacidae
 - Ogcocephalidae (Oncocephalidae, Onchocephalidae, Malthidae, Malthidae)
 - Suborder Ceratioidei
 - Melanocetidae
 - Diceratiidae (including Laevoceratiidae, Aeschynichthyidae)
 - Himantolophidae
 - Oneirodidae
 - Gigantactinidae
 - Neoceratiidae
 - Centrophrynidae
 - Ceratiidae
 - Caulophrynidae
 - Linophrynidae (including Photocorynidae, Aceratiidae)
- Order Gadiformes (Anacanthini, Macruriformes, Gadamorphi, Perciformes in part)
 - Suborder Muraenolepoidei
 - Muraenolepididae (Muraenolepidae)
 - Suborder Gadoidei
 - Moridae (including Eretmophoridae, Tripterophycidae)
 - Bregmacerotidae
 - Gadidae (including Gaidropsaridae, Ranicipitidae)
 - Merlucciidae
 - Suborder Ophidiioidei
 - Ophidiidae (including Brotulidae, Brotulophidae, Aphyonidae)
 - Carapidae (Fierasferidae, Disparichthyidae)
 - Pyramodontidae
 - Suborder Zoarcoidei
 - Zoarcidae (including Lycodidae, Lycodapodidae, Derepodichthyidae)
 - Suborder Macrouroidei
 - Macrouridae (Macruridae, Macrouroididae, Coryphaenoididae, including Lyconidae)
- SUPERORDER ATHERINOMORPHA**
 - Order Atheriniformes (Synentognathi, Beloniformes, Gambusiformes, Microcyprini in part, Cyprinodontiformes in part, Percosoces in part, Mugiliformes in part, Mugilomorphi in part, Phallostethiformes, Perciformes in part)
 - Suborder Exocoetoidei
 - Exocoetidae (including Hemiramphidae, Hemirhamphidae, Oxyporhamphidae, Evolantiidae)
 - Belonidae (Esocidae, Esocesidae as of Rafinesque, including Tylosuridae, Petalichthyidae)
 - Scomberesocidae (Scomberesocidae)
 - Suborder Cyprinodontoidei
 - Oryziatidae
 - Adrianichthyidae
 - Horaichthyidae
 - Cyprinodontidae (including Fundulidae, Orestiidae, Empetrichthyidae)
 - Goodeidae (including Characodontidae)
 - Anablepidae (Anablepsidae)
 - Jenynsiidae (Fitzroyiidae, Fitzroyidae)
 - Poeciliidae (including Tomeuridae)
 - Suborder Atherinoidei
 - Melanotaeniidae (including Zanteclidae, Neoatherinidae)
 - Atherinidae (including Bedotiidae, Pseudomugilidae)

Isonidae
 Neostethidae
 Phallostethidae

SUPERORDER ACANTHOPTERYGII

Order Beryciformes (Xenoberyces, Berycomorphi, Berycoidei in part, Stephanoberyciformes in part)

Suborder Stephanoberycoidei

Stephanoberycidae
 Melamphaeidae (Melamphaidae, Melamphasidae)
 Gibberichthyidae

Suborder Polymixioidei

Polymixiidae

Suborder Berycoidei

Diretmidae
 Trachichthyidae (including Hoplopterygidae, Sorosichthyidae)
 Korsogasteridae
 Anoplogasteridae (Caulolepidae)
 Berycidae
 Monocentridae
 Anomalopidae
 Holocentridae (Holocentridae)

Order Zeiformes (Zeomorphi, Zeoidei)

Parazenidae
 Macrurocyttidae (Zeniontidae)
 Zeidae (including Cyttidae, Cyttopsidae, Zenidae)
 Grammicolepididae (Grammicolepidae)
 Oreosomatidae
 Caproidae (Caprophonidae, including Antigoniidae)

Order Lampridiformes (Selenichthyes, Allotriognathi)

Suborder Lampridoidei

Lampridae (Lamprididae)

Suborder Veliferoidei

Veliferidae

Suborder Trachipteroidei

Lophotidae
 Trachipteridae (Trachypteridae)
 Regalecidae

Suborder Stylephoroidei

Stylephoridae (Stylophoridae)

Order Gasterosteiformes (Lophobranchii, Thoracostei, Aulostomi, Solenichthyes, Scleroparei in part, Syngnathiformes, Aulostomiformes, Rhamphosiformes)

Suborder Gasterosteoidi

Gasterosteidae (Sclerogenidae in part)
 Aulorhynchidae
 Indostomidae

Suborder Aulostomoidei

Aulostomidae
 Fistulariidae (Fistularidae)
 Macrorhamphosidae (Macroramphosidae, Rhamphosidae)
 Centriscidae (Amphisilidae)

Suborder Syngnathoidei

Solenostomidae (Solenostomatidae, Solenostomatichthyidae, including Solenichthyidae)
 Syngnathidae (including Hippocampidae, Siphostomidae)

Order Channiformes (Labyrinthici in part, Ophiocephaliformes)

Channidae (Ophicephalidae, Ophiocephalidae, including Parophiocephalidae)

Order Synbranchiformes (Symbranchia, Symbranchii, Symbranchiformes, Alabiformes)

Suborder Alabetoidei

Alabetidae (Alabidae, including Cheilobranchidae, Chilobranchidae)

Suborder Synbranchoidei

- Synbranchidae (Symbranchidae, including Flutidae, Monopteridae)
- Amphipnoidae
- Order Scorpaeniformes (Cataphracti in part, Scleroparei in part, Pareioplitae, Loricati, Sclerogeni, Cottomorphi, Perciformes in part)
- Suborder Scorpaenoidei
 - Scorpaenidae (Sclerogenidae in part, including Tetrarogidae)
 - Triglidae (Sclerogenidae in part, including Peristediidae, Peristediontidae)
 - Caracanthidae
 - Aploactinidae (Aploactidae, ?including Bathyaploactidae)
 - Synancejidae (Synanceidae)
 - Pataecidae (including Gnathanacanthidae)
- Suborder Hexagrammoidei
 - Hexagrammidae (including Ophiodontidae, Oxylebiidae, Chiridae)
 - Anoplopomatidae (Anoplopomidae, including Erilepidae)
 - Zaniolepididae (Zaniolepidae)
- Suborder Platycephaloidei
 - Platycephalidae (including Bembradidae, Bembridae, Parabembridae)
- Suborder Hoplichthyoidei
 - Hoplichthyidae (Oplichthyidae)
- Suborder Congiopodoidei
 - Congiopodidae (Agriopidae)
- Suborder Cottoidei
 - Icelidae (including Ereuniidae, Marukawichthyidae)
 - Cottidae (Sclerogenidae in part, including Jordaniidae, Blepsiidae, Blepsidae, Scorpaenichthyidae, Ascelichthyidae, Synchronidae, Rhampnocottidae, Hemitripterae, Neophrynichthyidae)
 - Cottomephoridae (including Abyssocottidae)
 - Comephoridae
 - Normanichthyidae
 - Cottunculidae
 - Psychrolutidae
 - Agonidae (including Aspidophoroididae, Aspidophoridae)
 - Cyclopteridae (including Liparopidae, Liparidae, Lipariidae, Eutelichthyidae, Rhodichthyidae, Cyclogasteridae)
- Order Dactylopteriformes (in part Craniomi, Scleroparei, Cataphracti, and Perciformes)
 - Dactylopteridae (Cephalacanthidae)
- Order Pegasiformes (Hypostomides, Perciformes in part)
 - Pegasidae
- Order Perciformes (Percomorphi in part, Holconoti, Labyrinthici in part, Chromides, Pharyngognathi, Gobioidae, Jugulares in part, Malacichthyes, Icosteiformes, Percosoces in part, Mugiliformes in part, Polynemiformes, Rhegnopteri, Bathyclupeiformes, Xenoberyces in part, Berycoidei in part, Beryciformes in part, Thunniformes, Plecostei, Scombriformes, Echeneiformes, Discocephali, Mastacembeliformes, Opisthomi, Chaudhuriiformes, Anabantiformes, Blenniiformes, Trachiniformes, Gobiiformes, Carangiformes, Acanthuriformes, Squamipenes, Embiotocomorphi, Gadopseiformes, Coryphaeniformes, Amphiprioniformes)
 - Suborder Percoidei
 - Centropomidae (Oxylabracidae, including Latidae, Chandidae, Ambassidae, Ambassiidae)
 - Serranidae (including Percichthyidae, Chromileptidae, Perciliidae, Moronidae, Oligoridae, Maccullochellidae, Macquariidae, Niphonidae, Plectroplitidae, Epinephelidae, Cephalopholidae, Bostockiidae, Diploprionidae, Rainfordiidae, Hypoplectrodidae, Plectropomidae, Anthiidae, Ostracoberycidae, Paracentropristidae)
 - Grammistidae (including Rypiticidae)
 - Pseudochromidae
 - Pseudogrammidae (including Rhegmatidae)
 - Grammidae (including Stigmatonotidae)
 - Plesiopidae (including Pharoptyercidae)
 - Pseudoplesiopidae
 - Anisochromidae
 - Acanthoclinidae

Glaucosomidae

Theraponidae (Teraponidae, Terapontidae, Tesapontidae)

Banjosidae

Kuhliidae (Duleidae, including Nannatherinidae, Nannopercidae)

Gregoryinidae (?based on young of cheilodactylid)

Centrarchidae (including Elassomatidae, Elassomidae, Cristidae, Grystidae, Micropteridae, Eucentrarchidae)

Priacanthidae

Apogonidae (including Ostorhinchidae, Gymnapogonidae, Apogonichthyidae, Henicichthyidae, Henichthyidae, Dinolestidae, Cheilodipteridae, "Amiidae," Epigonidae)

Acropomatidae (Acropomatidae)

Percidae (including Etheostomatidae, Etheostomidae)

Sillaginidae

Branchiostegidae (Latilidae, including Malacanthidae)

Labracoglossidae

Lactariidae

Pomatomidae (including Scombropidae, Scombropsidae)

Rachycentridae (Rhachycentridae, Elacatidae)

Echeneidae (Echeneididae)

Carangidae (including Seriolidae, Nematistiidae, Juvenellidae)

Coryphaenidae

Formionidae (Formiidae, Apolectidae)

Menidae

Leiognathidae (Liognathidae, including Equulidae)

Bramidae (including Steinegeriidae, Trachyberycidae, Pteraclididae, Pteraclidae, Lepidotidae, Lepodidae)

Cristiidae (Elephenoridae)

Arripidae (Arripididae)

Emmelichthyidae (including Erythrichthyidae, Erythroclidae, Dipterygonotidae, Inermiidae, Maenidae, Spicaridae, Merolepidae, Centracanthidae, Centracantidae)

Lutjanidae (Lutianidae, Luthianidae, including Hoplopagridae, Etelidae, Verilidae, Aphareidae, Caesionidae, Caesiodidae)

Nemipteridae (including Scolopsidae)

Lobotidae

Gerridae (including Eucinostomidae, Xystaemidae)

Pomadasyidae (Pomadasiidae, Haemulidae, Haemulonidae, including Gaterinidae, Pristipomidae, Pristipomatidae, Plectorhynchidae, Xenichthyidae)

Lethrinidae (including Monotaxidae, Neolethrinidae)

Pentapodidae

Sparidae (including Denticidae, Pimelepteridae, Paradicichthyidae, Paradichthyidae)

Sciaenidae (including Otolithidae)

Mullidae

Monodactylidae (Psettidae)

Pempheridae (including Leptobramidae)

Bathylupeiidae

Toxotidae

Coracinidae (Dichistiidae)

Kyphosidae (Cyphosidae, including Scorpionidae, Scorpidae, Parascorpionidae, Girellidae)

Ehippidae (including Chaetodipteridae, Platacidae, Ilarchidae, Drepanidae, Drepanichthyidae)

Scatophagidae (including Prenidae)

Rhinoprenidae

Chaetodontidae (including Pomacanthidae)

Enoplosidae

Pentacerotidae (Histiopteridae)

Nandidae (including Polycentridae, Pristolepidae)

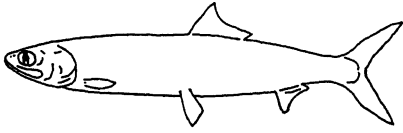
Oplegnathidae (Hoplegnathidae)

Embiotocidae (Ambiotocidae, including Ditremidae, Hystero carpidae, Holconotidae)

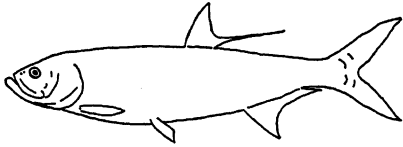
- Cichlidae (Chromidae, not a pomacentrid)
- Pomacentridae (Abudefdufidae, Glyphiodontidae, Ctenolabridae, including Amphiprionidae, Chromidae, Premnidae)
- Gadopsidae
- Cirrhitidae
- Chironemidae
- Aplodactylidae (Haplodactylidae)
- Cheilodactylidae
- Latridae (Latrididae)
- Owstoniidae
- Cepolidae
- Suborder Mugiloidei
 - Mugilidae
- Suborder Sphyraenoidei
 - Sphyraenidae
- Suborder Polynemoidei
 - Polynemidae
- Suborder Labroidei
 - Labridae (Cyclolabridae, including Coridae, Neolabridae, Bodianidae, Harpidae)
 - Odacidae (including Siphonognathidae, Neodaciidae, Neodacidae)
 - Scaridae (Callyodontidae, including Sparisomidae, Scarichthyidae)
- Suborder Trachinoidei
 - Trichodontidae
 - Opisthognathidae
 - Bathymasteridae
 - Mugiloididae (including Pinguipedidae, Parapercidae, Parapercichthyidae)
 - Cheimarrichthyidae (Chimarrichthyidae, not a catfish)
 - Trachinidae (including Callipterygidae)
 - Percophididae (Percophidae, including Bembropsidae, Bembropidae, Pteropsaridae, Hemero-coetidae)
 - Trichonotidae
 - Creediidae
 - Limnichthyidae (Limnichthidae)
 - Oxudercidae
 - Leptoscopidae
 - Dactyloscopidae
 - Uranoscopidae (including Astroscopidae, Pleuroscopidae)
 - Champsodontidae
 - Chiasmodontidae
- Suborder Notothenioidei
 - Bovichthyidae (Bovichtidae, Bovictidae, Pseudaphritidae)
 - Nototheniidae (including Harpagiferidae, Gelididae)
 - Bathydraconidae
 - Channichthyidae (Channichthyidae, Chaenichthyidae)
- Suborder Blennioidei
 - Blenniidae (including Runulidae, Salariidae, Atopoclinidae, Xiphasiidae, Nemophilidae)
 - Anarrhichadidae (Anarrhichadidae, including Anarrhichthyidae)
 - Xenocephalidae
 - Congrogadidae (including Halidesmidae, Haliophidae)
 - Notograptidae (including Stichariidae)
 - Peronedysidae (Peronedysidae)
 - Ophioclinidae (Ophioclinidae)
 - Tripterygiidae (Tripterygiidae)
 - Clinidae (including Paraclinidae, Xenopoclinidae)
 - Chaenopsidae (including Emblemariidae)
 - Stichaeidae (including Lumpenidae, Xiphisteridae, Xiphidiontidae, Chirolophidae, Cebedichthyidae, Cryptacanthodidae, Cryptacanthidae)
 - Ptilichthyidae

- Pholididae (Pholidae, including Opisthocentridae)
- Scytalinidae (Scytaliscidae)
- Zaproridae
- Suborder Icosteoidi
 - Icosteidae (Acrotidae)
- Suborder Schindlerioidei
 - Schindleriidae
- Suborder Ammodytoidei
 - Ammodytidae (including Bleekeridae, Bleekeriidae)
 - Hypoptychidae
- Suborder Callionymoidei
 - Callionymidae (including Draconettidae)
- Suborder Gobioidi
 - Gobiidae (including Eleotridae, Milyeringidae, Dollichthyidae, Benthophilidae, Gobiomoridae, Sicydiaphiidae, Apocrypteidae, Periophthalmidae)
 - Rhyacichthyidae (Platypteridae)
 - Kraemeriidae (Psammichthyidae)
 - Gobioididae (including Amblyopidae, Taenioidae, Taenioididae)
 - Trypauchenidae
 - Microdesmidae (Cerdalidae, including Pholidichthyidae, Gunnellichthyidae, Paragobioididae)
- Suborder Kurtoidei
 - Kurtidae
- Suborder Acanthuroidei
 - Acanthuridae (Hepatidae, Acronuridae, Harpuridae, Teuthidae, Teuthididae in part, including Zanclidae, Nasidae)
 - Siganidae (Theutyidae, Teuthididae in part, Amphacanthidae)
- Suborder Scombroidei
 - Gempylidae (Acinaceidae, including Lemnisomidae, Ruvettidae)
 - Trichiuridae (including Lepidopidae)
 - Scombridae (Scomberidae, including Cybiidae, Cibiidae, Thunnidae, Katsuwonidae, Scomberomoridae, Sardidae, Acanthocybiidae, Gasterochismidae)
 - Xiphiidae
 - Luvaridae (Dianidae)
 - Istiophoridae (Histiophoridae, including Tetrapturidae, Makairidae)
- Suborder Stromateoidi
 - Centrolophidae (including Icichthyidae)
 - Nomeidae (Psenidae)
 - Stromateidae (Pampidae)
 - Tetragonuridae
- Suborder Anabantoidei
 - Anabantidae
 - Belontiidae (Belontidae, Polyacanthidae)
 - Helostomatidae (Helostomidae)
 - Osphronemidae (Osphromenidae, Labyrinthidae)
- Suborder Luciocephaloidei
 - Luciocephalidae
- Suborder Mastacembeloidei
 - Mastacembelidae (Rhynchobdellidae)
 - Chaudhuriidae
- Order Pleuronectiformes (Heterosomata)
 - Suborder Psettoidi
 - Psettodidae
 - Suborder Pleuronectoidei
 - Citharidae
 - Scophthalmidae
 - Bothidae (including Paralichthyidae)
 - Pleuronectidae (Planidae, including Hippoglossidae, Samaridae, Paralichthodidae, Rhombosoleidae)

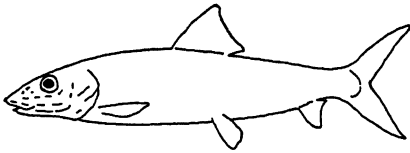
- Suborder Soleoidei
 - Soleidae (including Achiridae, Trinectidae, Synapturidae)
 - Cynoglossidae
- Order Tetraodontiformes (Plectognathi, Diodontomorphi)
 - Suborder Balistoidei
 - Triacanthidae (including Triacanthodidae)
 - Balistidae (including Monacanthidae, Aluteridae, Aleuteridae, Psilocephalidae, Anacanthidae, not a sting ray)
 - Ostraciontidae (Ostraciidae, including Aracnidae)
 - Suborder Tetraodontoidei
 - Tetraodontidae (Tetrodontidae, Gymnodontidae, including Lagocephalidae, Chonarhinidae, Xenopteridae, Canthigasteridae, Tropicichthyidae, Ovoididae, Colomesidae, Sphoeroididae)
 - Triodontidae
 - Diodontidae
 - Molidae (Orthagoriscidae, Triuridae)



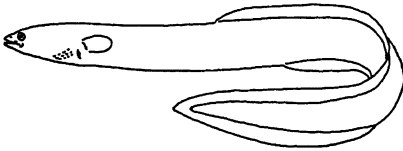
Elopidae



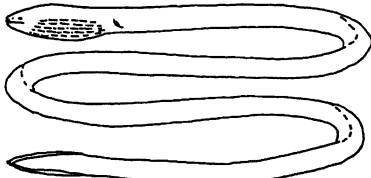
Megalopidae



Albulidae



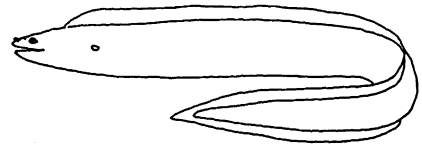
Anguillidae



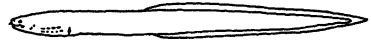
Moringuidae



Xenocoegradae



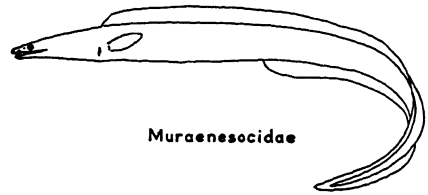
Muraenidae



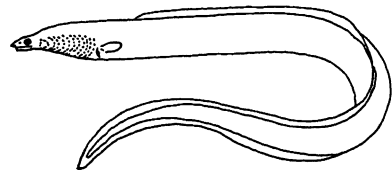
Heterenchelyidae



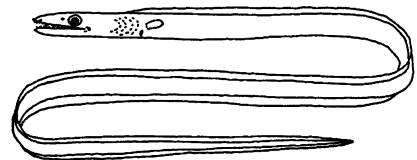
Dysommidae



Muraenesocidae

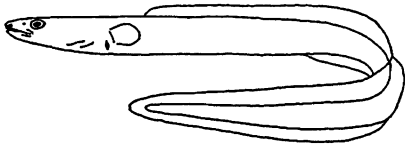


Neenchelyidae



Nettastomatidae

CHART 1.



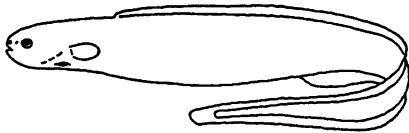
Congridae



Ophichthidae



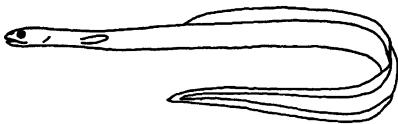
Synphobranchidae



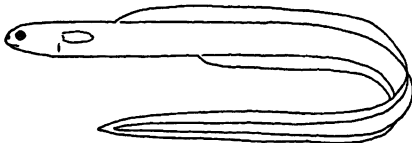
Simenchelyidae



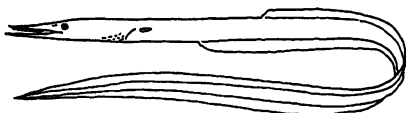
Dysommidae



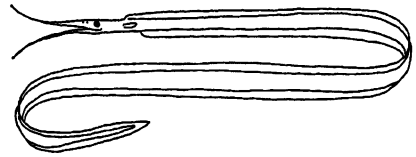
Derichthyidae



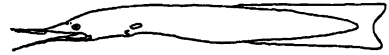
Macrocephenchylidae



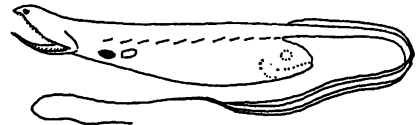
Serrivomeridae



Nemichthyidae



Cyemidae



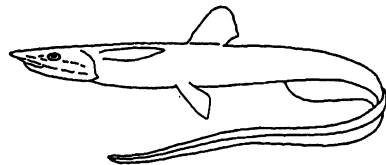
Saccopharyngidae



Eurypharyngidae



Monognathidae



Halosauridae

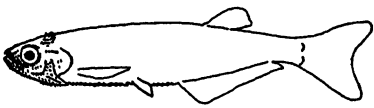


Lipogenyidae

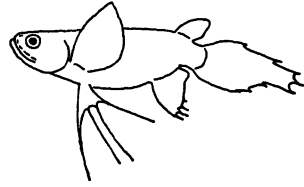


Notacanthidae

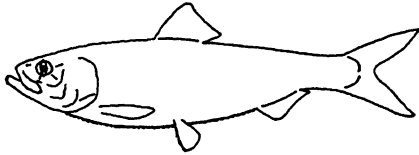
CHART 2.



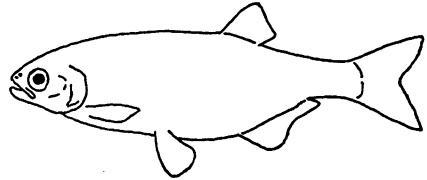
Denticipitidae



Pantodontidae



Clupeidae



Hiodontidae



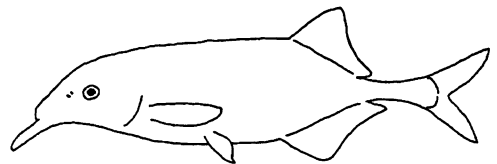
Engraulidae



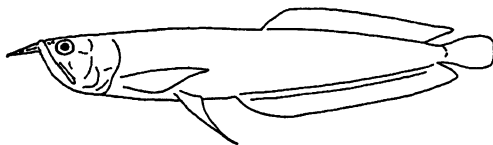
Notopteridae



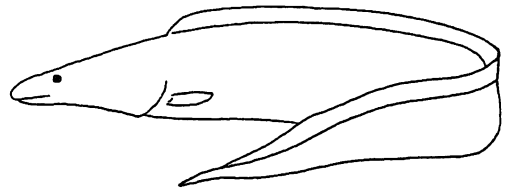
Chirocentridae



Mormyridae

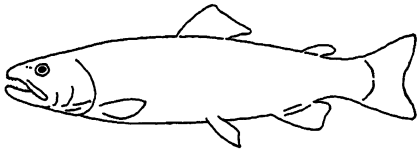


Osteoglossidae

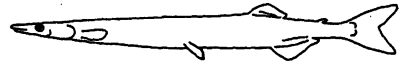


Gymnarchidae

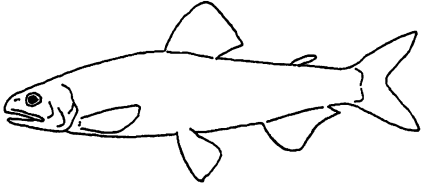
CHART 3.



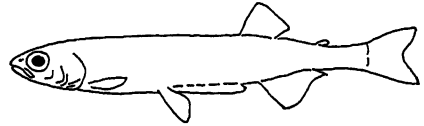
Salmonidae



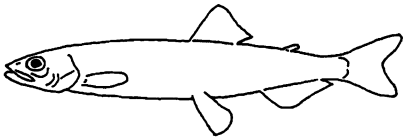
Salangidae



Plecoglossidae



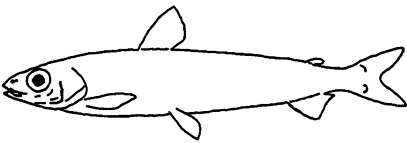
Retropinnidae



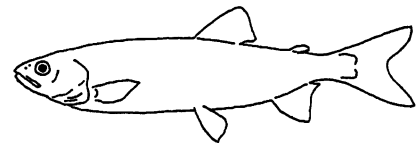
Osmeridae



Galaxiidae



Argentinidae



Aplochitonidae



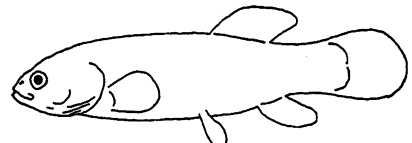
Bathylagidae



Esocidae

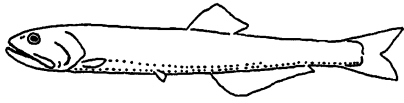


Opisthoproctidae

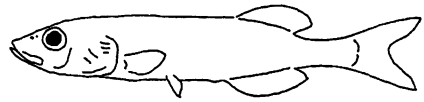


Umbridae

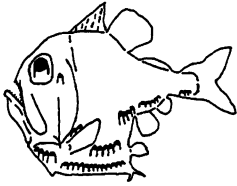
CHART 4.



Gonostomatidae



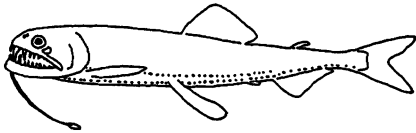
Alepocephalidae



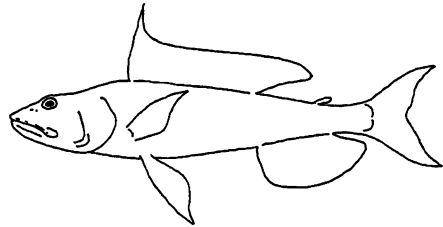
Sternoptychidae



Bathylaconidae



Astronesthidae



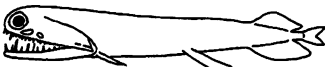
Aulopidae



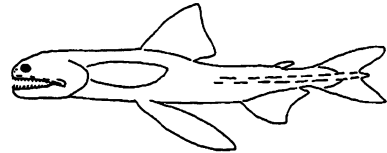
Melanostomiidae



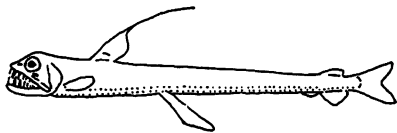
Synodontidae



Malacosteidae



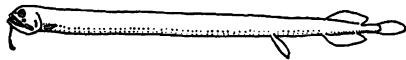
Harpadontidae



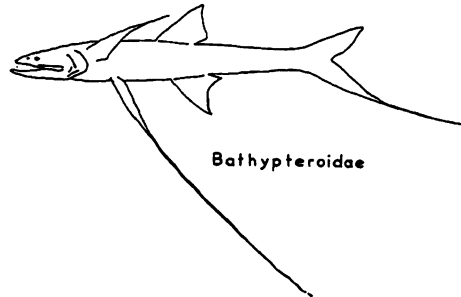
Chauliodontidae



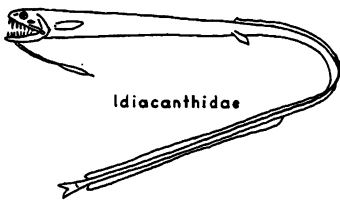
Chlorophthalmidae



Stomiidae



Bathypteroidae

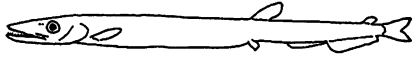


Idiacanthidae

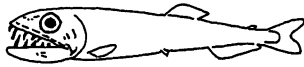
CHART 5.



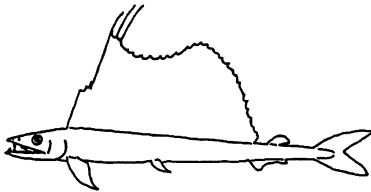
Ipnopidae



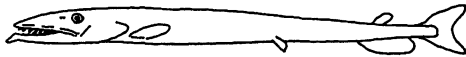
Paralepididae



Omosudidae



Alepisauridae



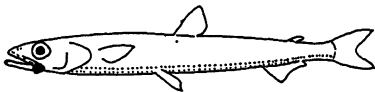
Anopteridae



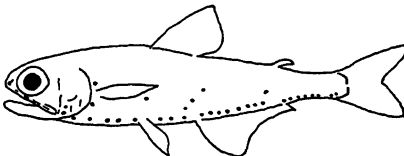
Evermannellidae



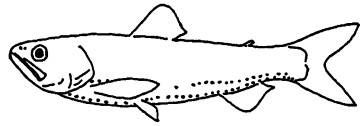
Scopelarchidae



Scopelosauridae



Myctophidae



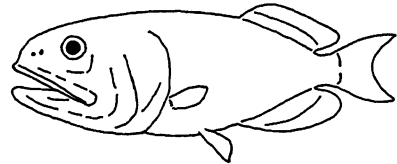
Neoscopelidae



Cetomimidae



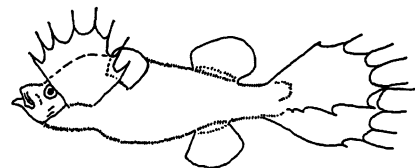
Barbourisidae



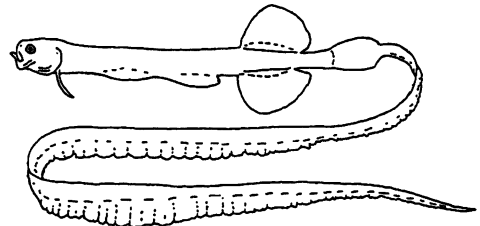
Rondeletiidae



Ateleopodidae

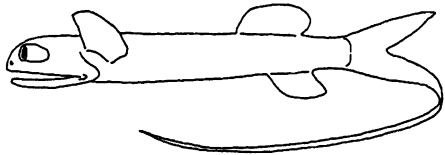


Mirapinnidae

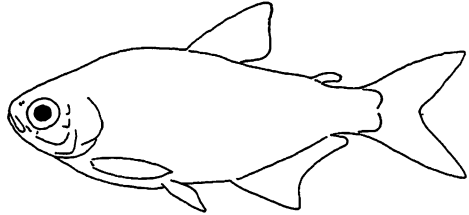


Eutaeniophoridae

CHART 6.



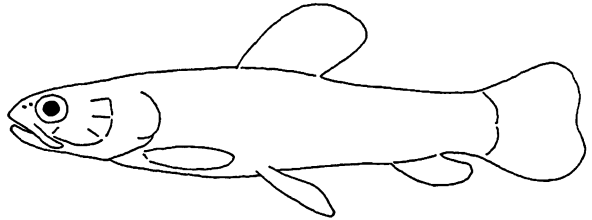
Giganturidae



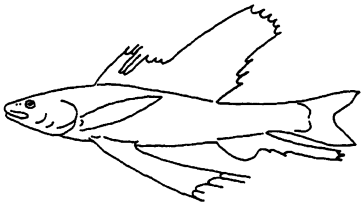
Characidae



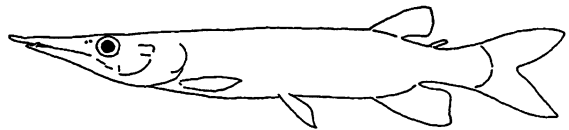
Rosauridae



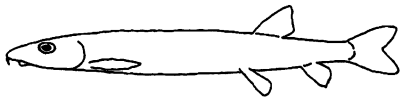
Erythrinidae



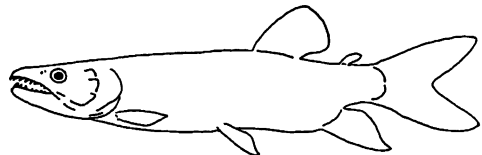
Macristiidae



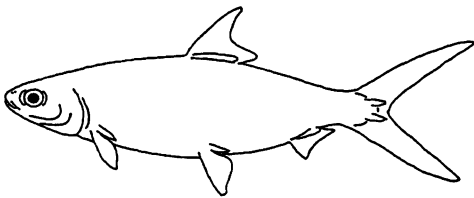
Ctenoluciidae



Gonorynchidae



Hepsetidae



Chanidae



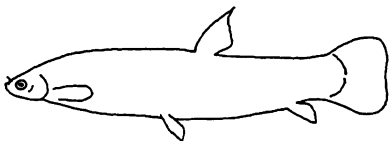
Cynodontidae



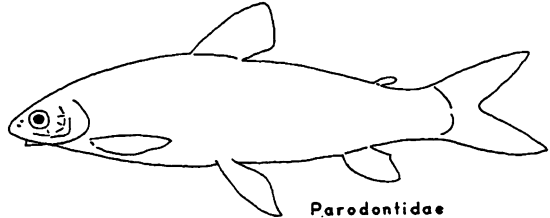
Kneriidae



Lebiasinidae



Phractolaemidae



Parodontidae

CHART 7.

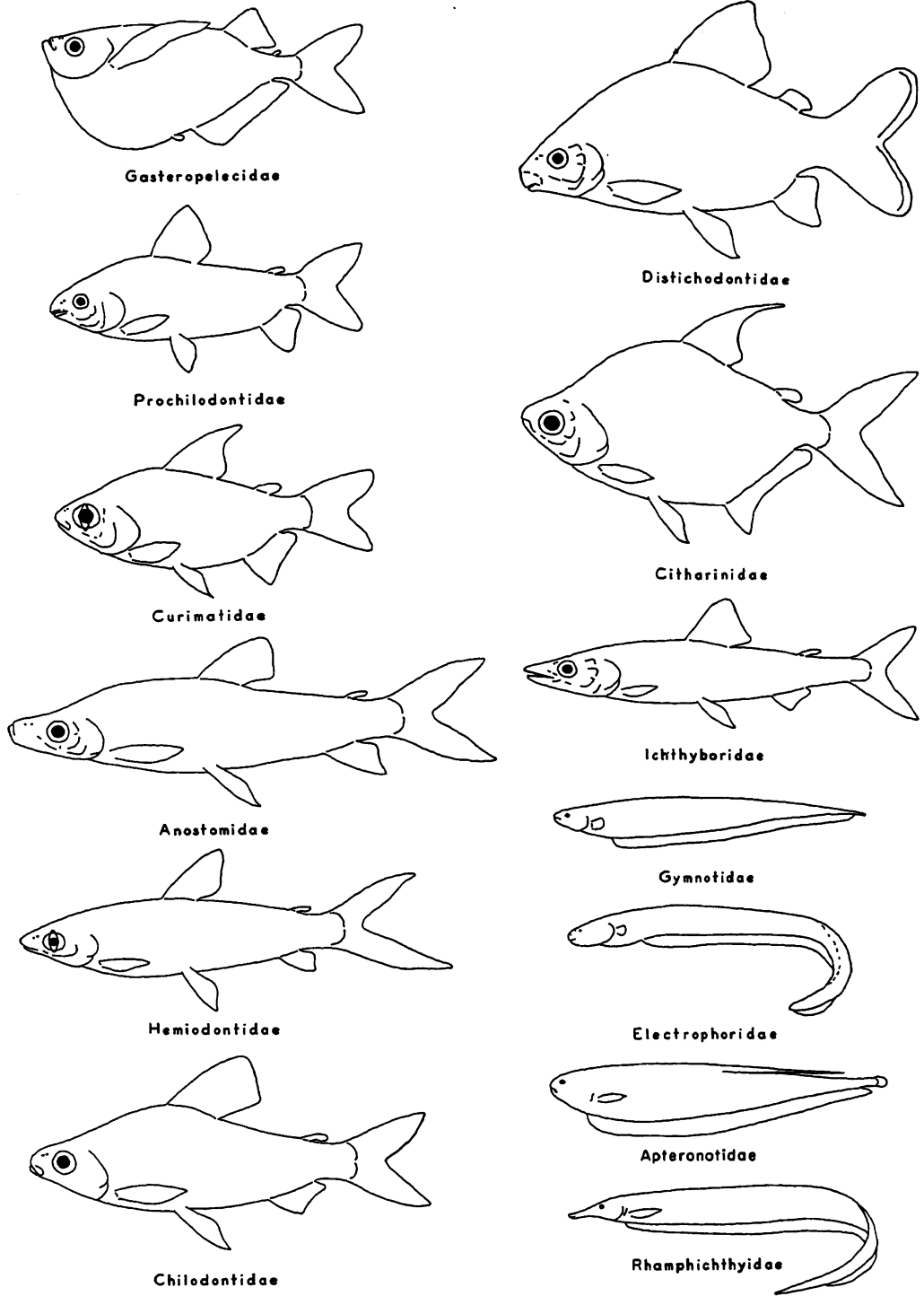
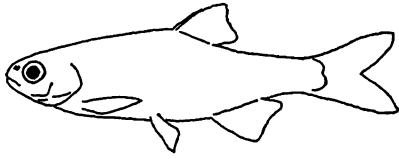
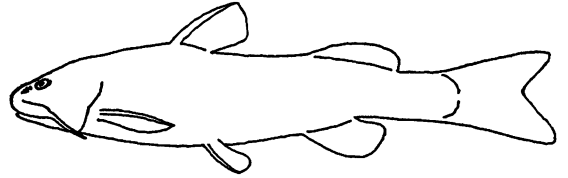


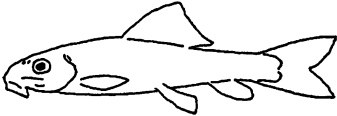
CHART 8.



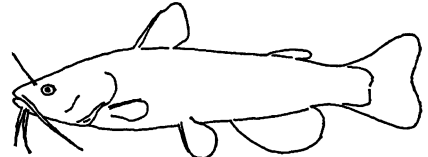
Cyprinidae



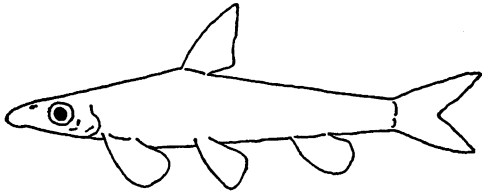
Diplomystidae



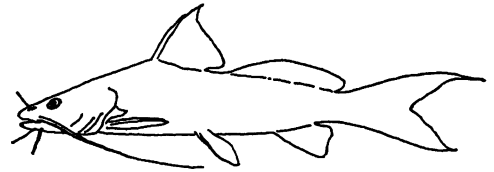
Gyrinocheilidae



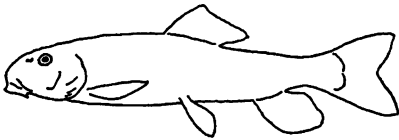
Ictaluridae



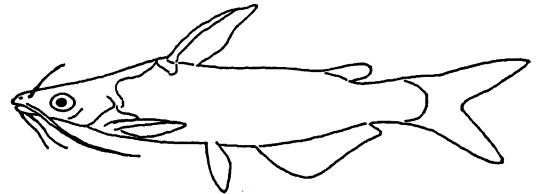
Psilorhynchidae



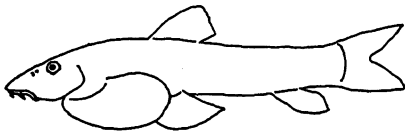
Bagridae



Catostomidae



Cranoglanididae



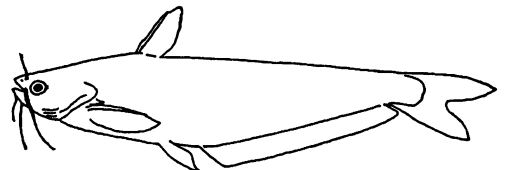
Homalopteridae



Siluridae

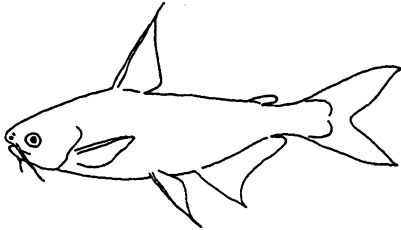


Cobitidae

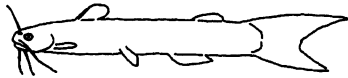


Schilbeidae

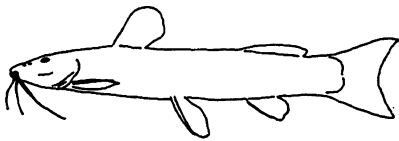
CHART 9.



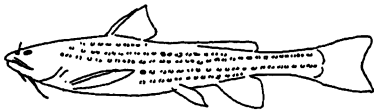
Pangasiidae



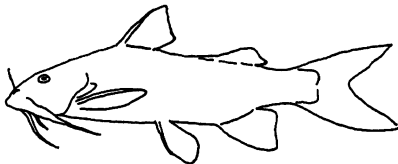
Amblycipitidae



Amphiliidae



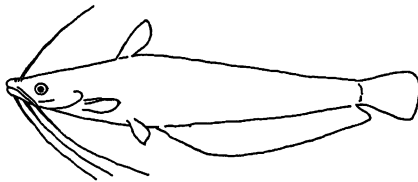
Akysidae



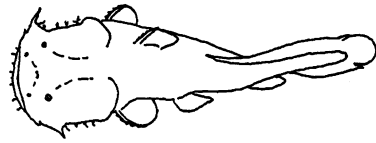
Sisoridae



Clariidae



Heteropneustidae



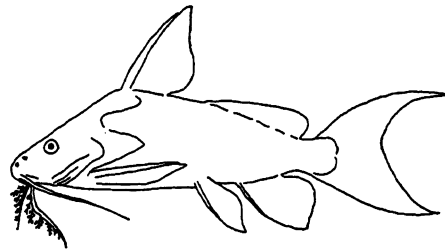
Chacidae



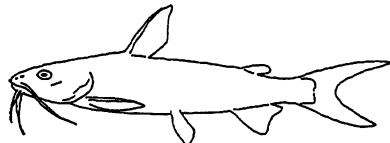
Olyridae



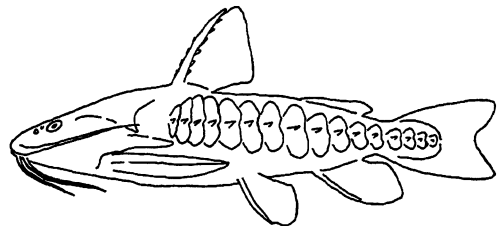
Malapteruridae



Mochokidae

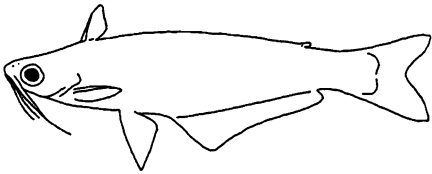


Ariidae

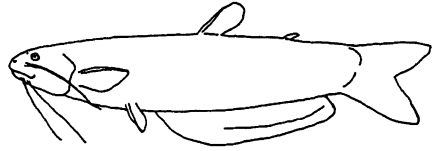


Doradidae

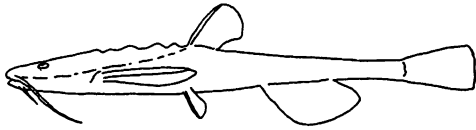
CHART 10.



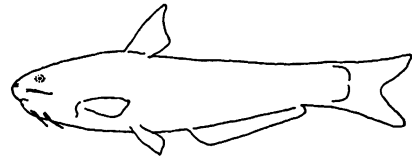
Auchenipteridae



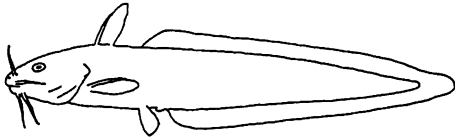
Helogeneidae



Aspredinidae



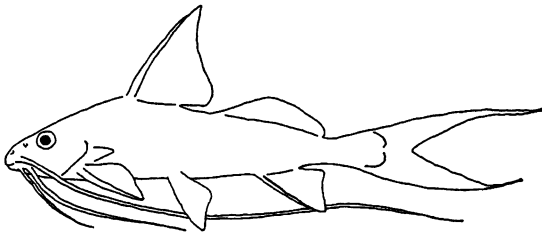
Cetopsidae



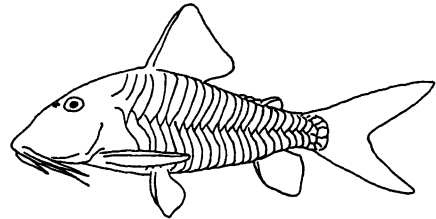
Plotosidae



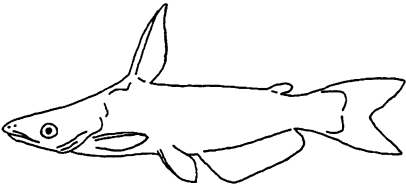
Trichomycteridae



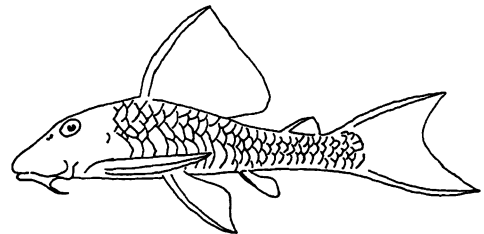
Pimelodidae



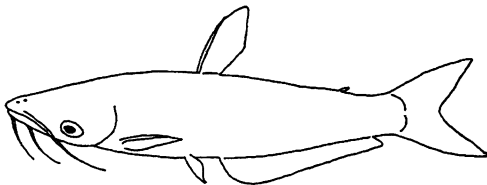
Callichthyidae



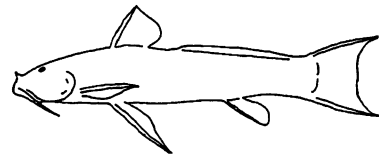
Ageneiosidae



Loricariidae



Hypophthalmidae

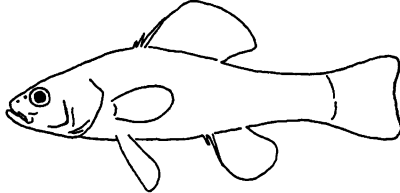


Astroblepidae

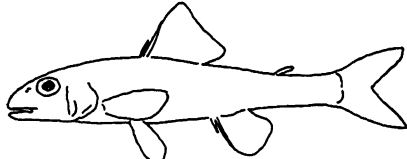
CHART 11.



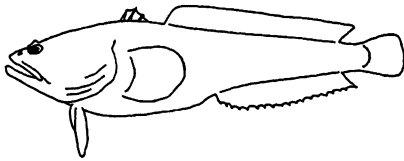
Amblyopsidae



Aphredoderidae



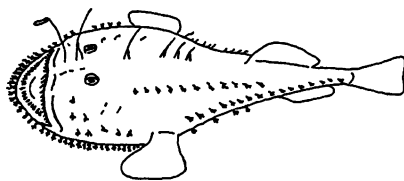
Percopsidae



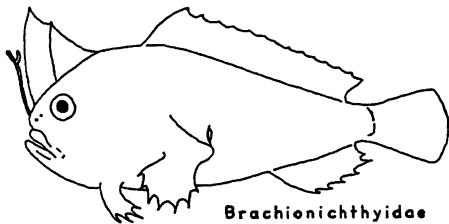
Batrachoididae



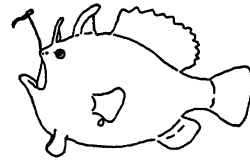
Gobiesocidae



Lophiidae



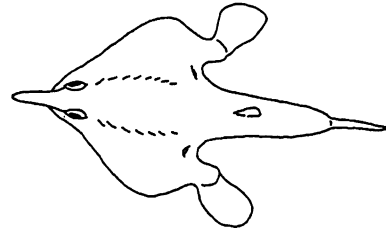
Brachionichthyidae



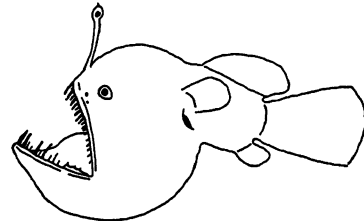
Antennariidae



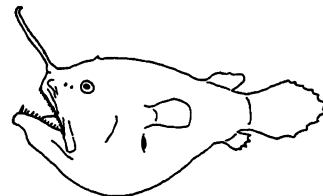
Chaunacidae



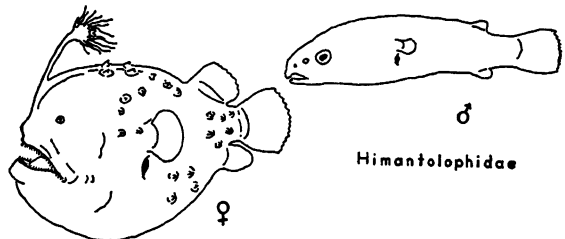
Ogcocephalidae



Melanocetidae



Diceratiidae

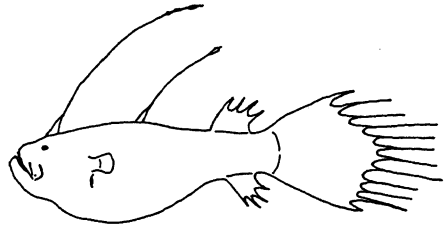


Himantolophidae

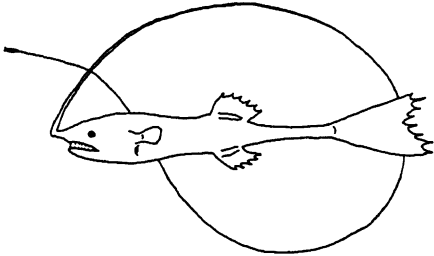
CHART 12.



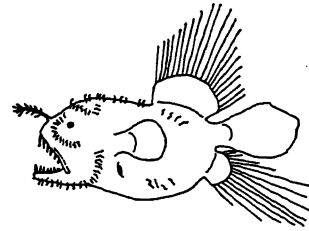
Oneirodidae



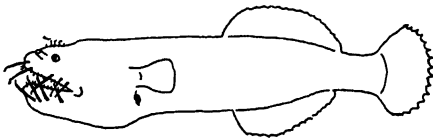
Ceratiidae



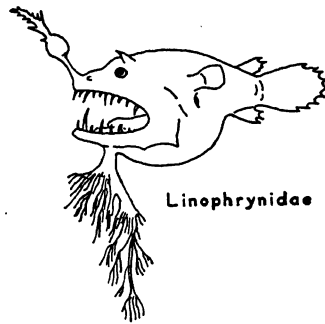
Gigantactinidae



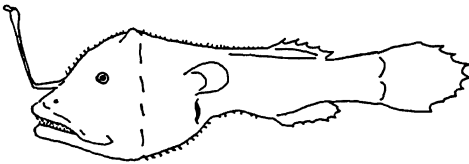
Caulophrynidae



Neoceratiidae

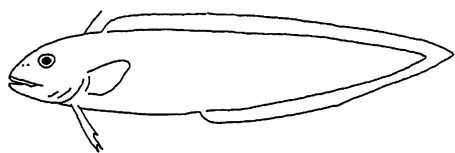


Linophrynidae

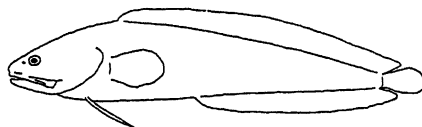


Centrophrynidae

CHART 13.



Muraenolepididae



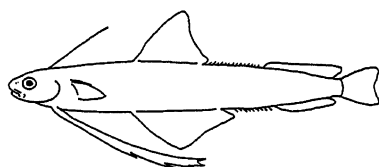
Ophidiidae



Moridae



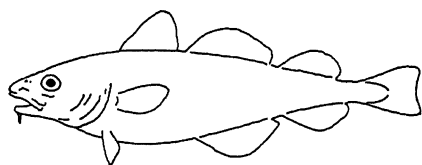
Carapidae



Bregmacerotidae



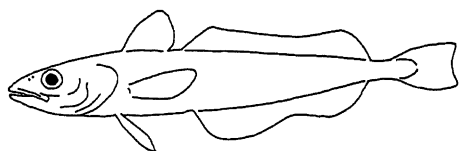
Pyramodontidae



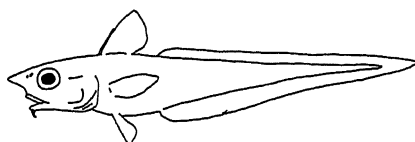
Gadidae



Zoarcidae



Merlucciidae



Macrouridae

CHART 14.

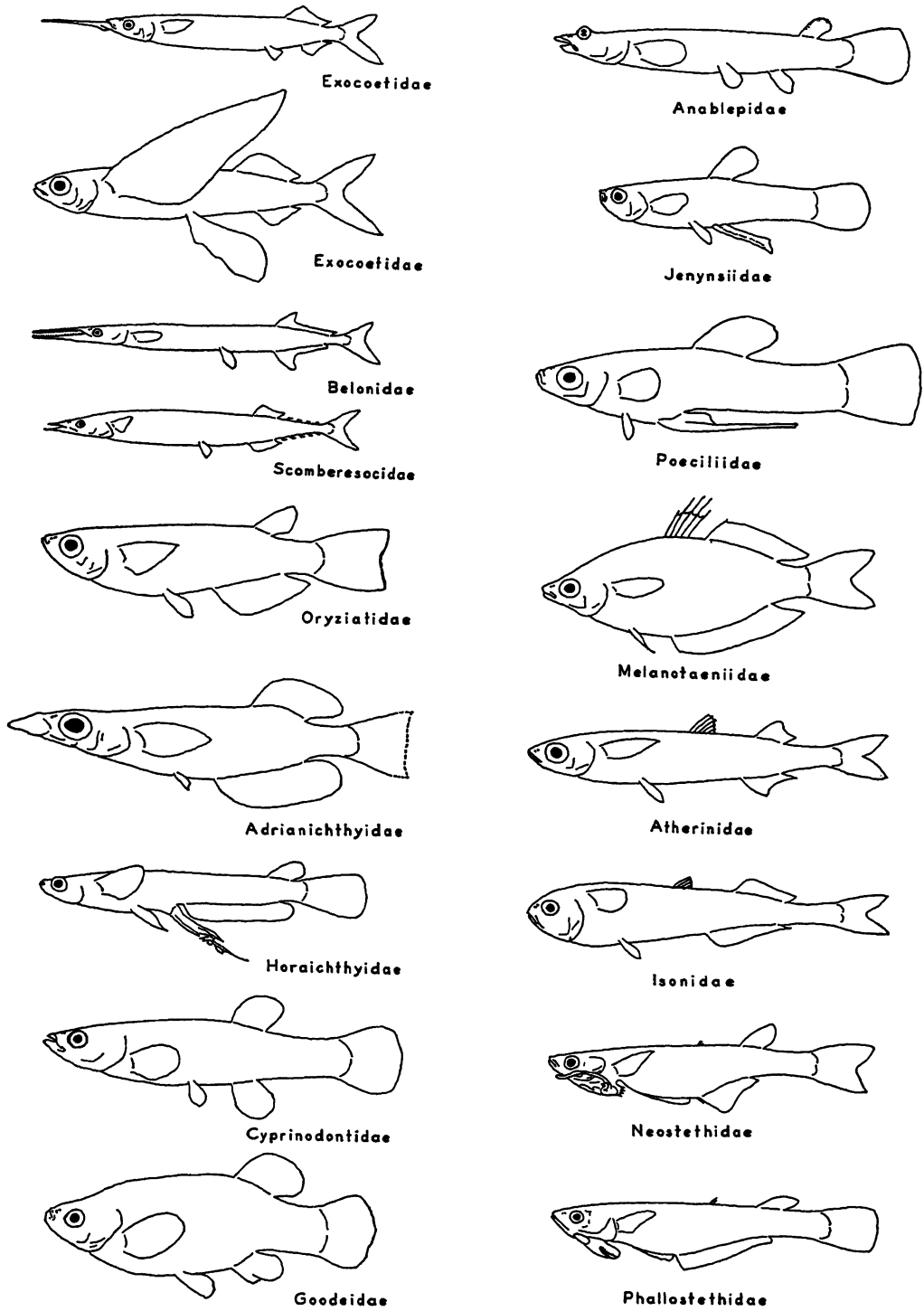


CHART 15.



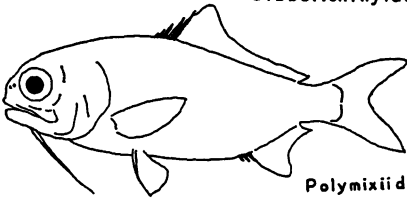
Stephanoberycidae



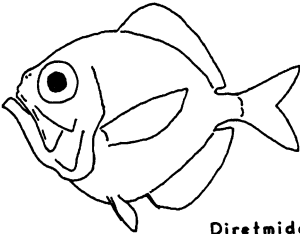
Melamphaeidae



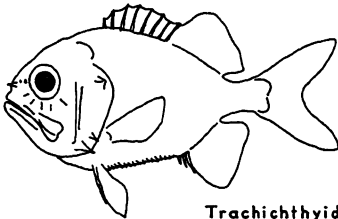
Gibberichthyidae



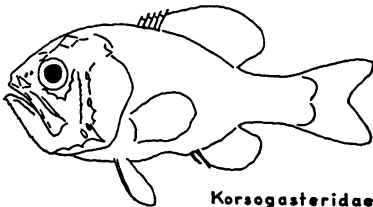
Polymixiidae



Diretmidae



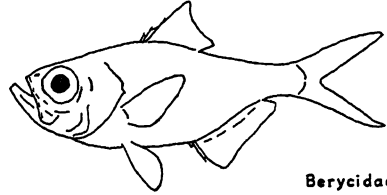
Trachichthyidae



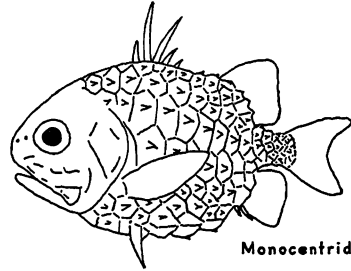
Korsogasteridae



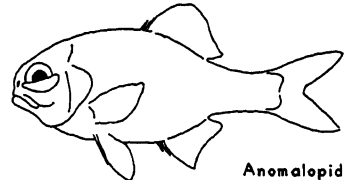
Anoplogasteridae



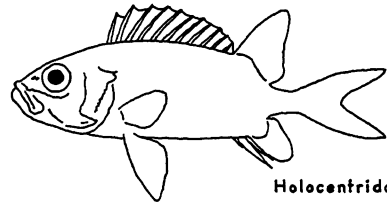
Berycidae



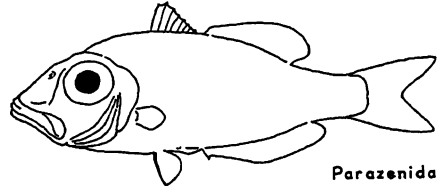
Monocentridae



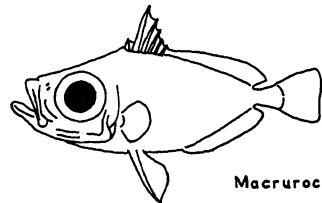
Anomalopidae



Holocentridae

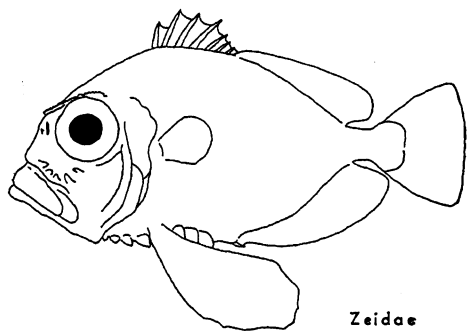


Parazenidae

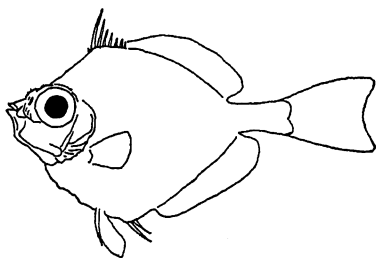


Macrurocyttidae

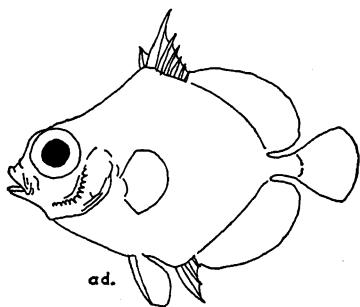
CHART 16.



Zeidae



Grammicolepididae

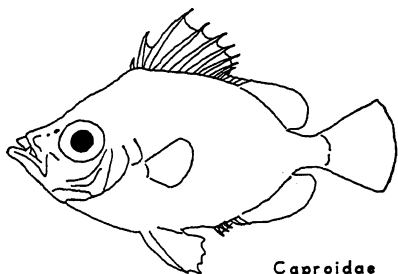


ad.

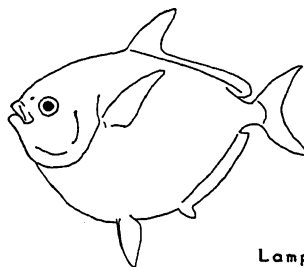
Oreosomatidae



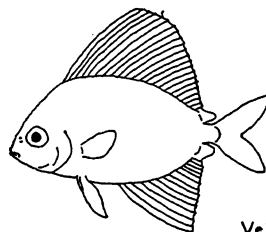
juv.



Caproidae



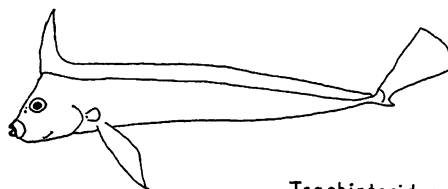
Lampridae



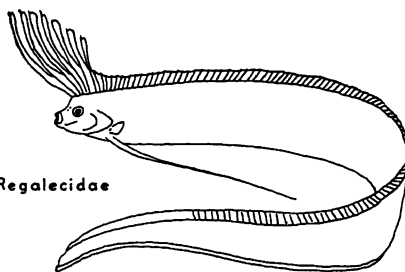
Veliferidae



Lophotidae



Trachipteridae

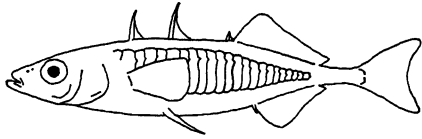


Regalecidae

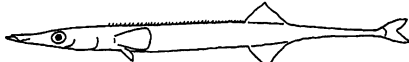


Stylephoridae

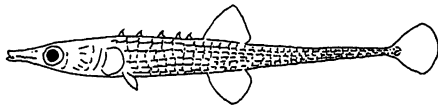
CHART 17.



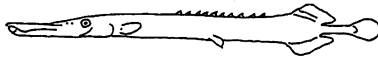
Gasterosteidae



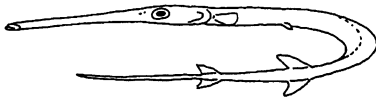
Aulorhynchidae



Indostomidae



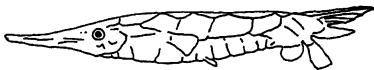
Aulostomidae



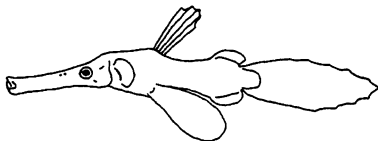
Fistulariidae



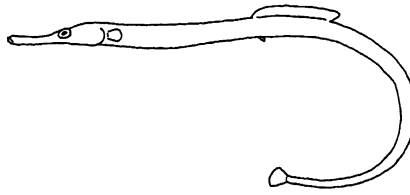
Macrorhamphosidae



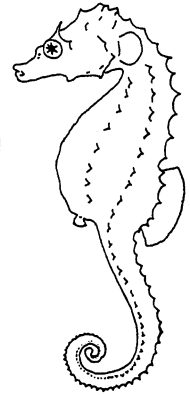
Centriscidae



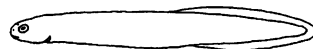
Solenostomidae



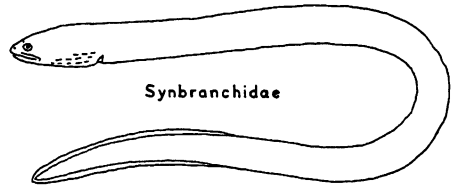
Syngnathidae



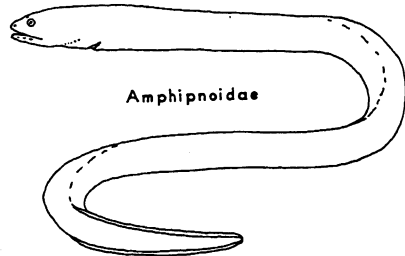
Channidae



Alabetidae

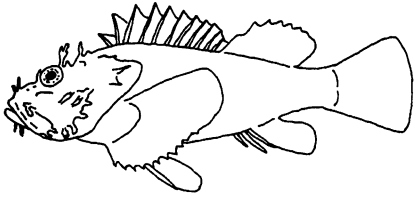


Synbranchidae

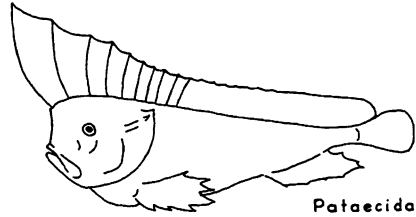


Amphipnoidae

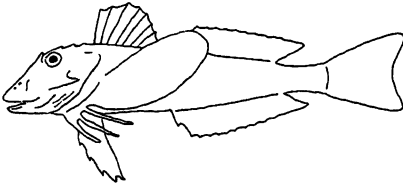
CHART 18.



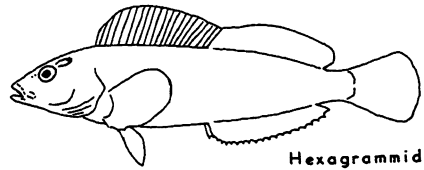
Scorpaenidae



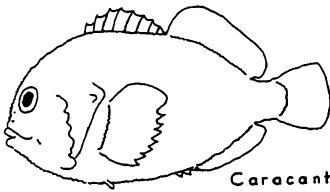
Pataecidae



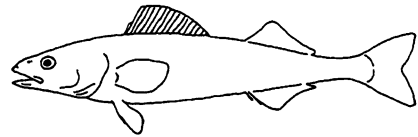
Triglidae



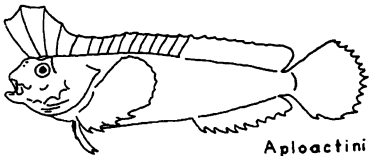
Hexagrammidae



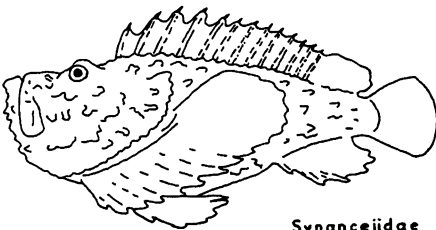
Caracanthidae



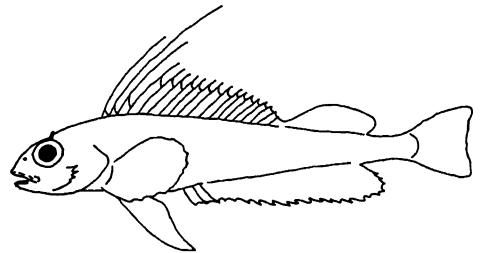
Anoplopomatidae



Aploactinidae

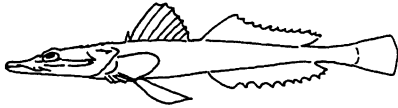


Synancejidae

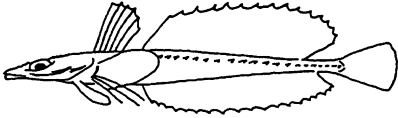


Zaniolepididae

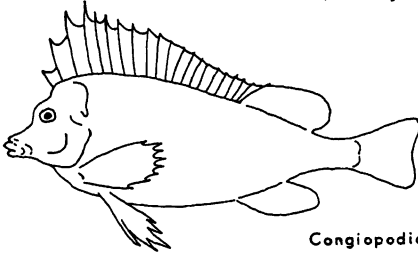
CHART 19.



Platycephalidae



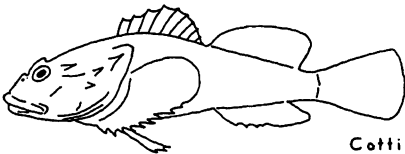
Hoplichthyidae



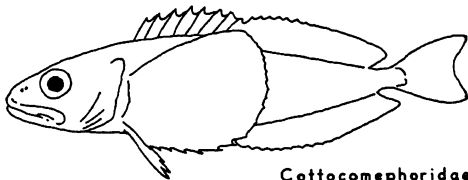
Congiopodidae



Icelidae



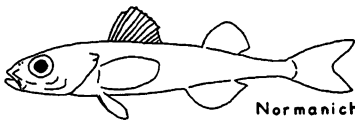
Cottidae



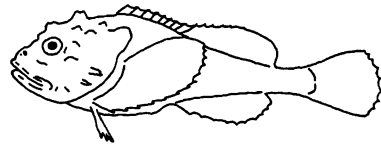
Cottocomphoridae



Comphoridae



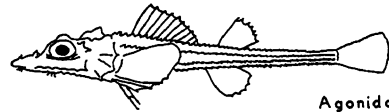
Normanichthyidae



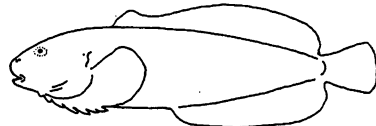
Cottunculidae



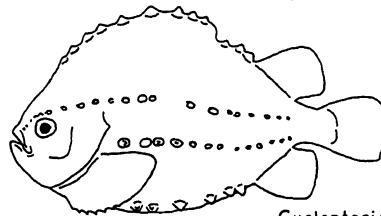
Psychrolutidae



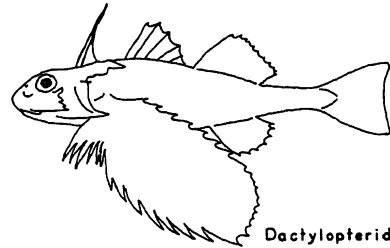
Agonidae



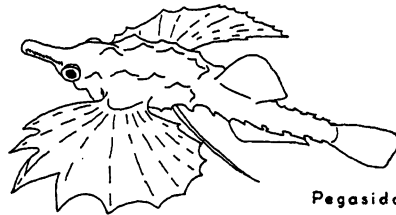
Cyclopteridae



Cyclopteridae

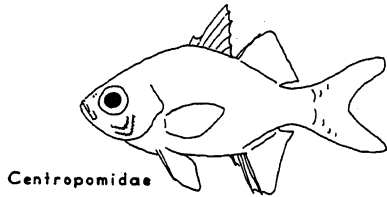


Dactylopteridae

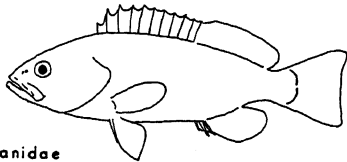


Pegasidae

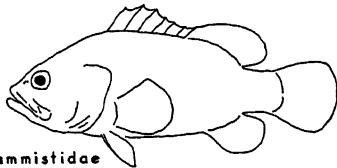
CHART 20.



Centropomidae



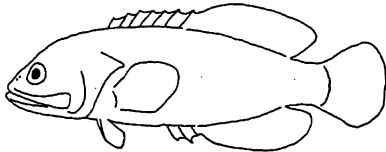
Serranidae



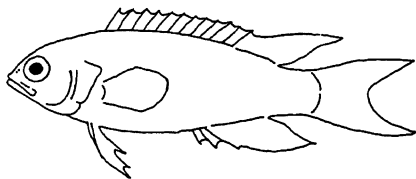
Grammistidae



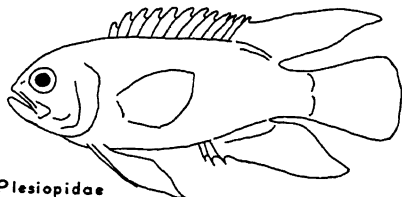
Pseudochromidae



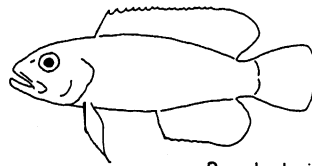
Pseudogrammidae



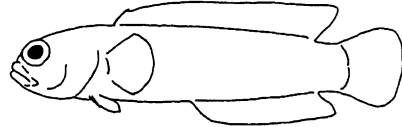
Grammidae



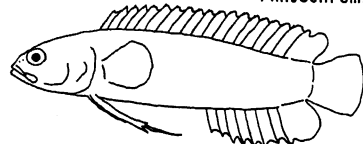
Plesiopidae



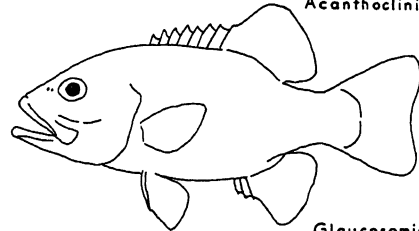
Pseudoplesiopidae



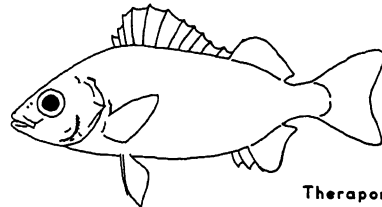
Anisochromidae



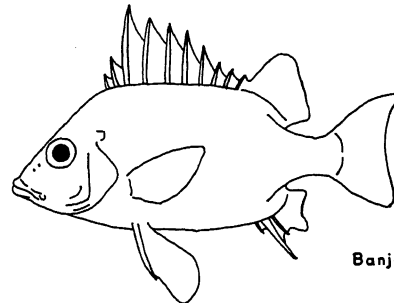
Acanthoclinidae



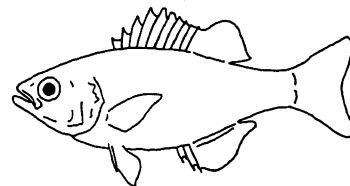
Glaucosomidae



Theraponidae

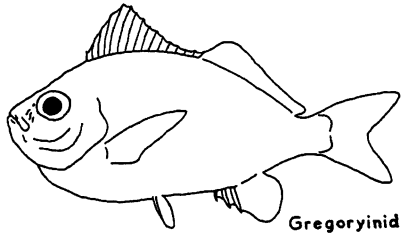


Banjosidae

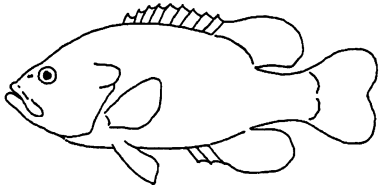


Kuhliidae

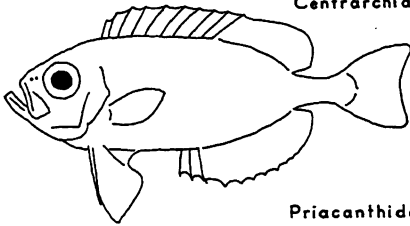
CHART 21.



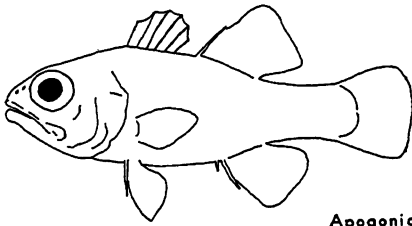
Gregoryinidae



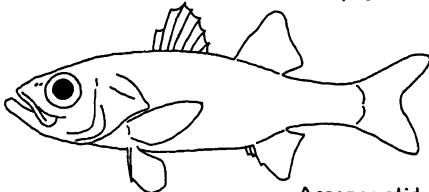
Centrarchidae



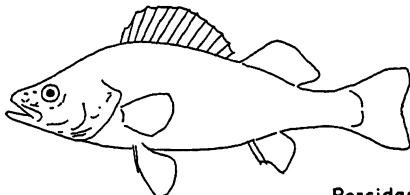
Priacanthidae



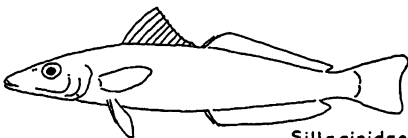
Apogonidae



Acropomatidae



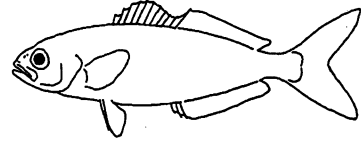
Percidae



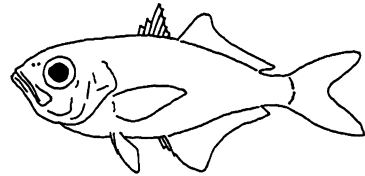
Sillaginidae



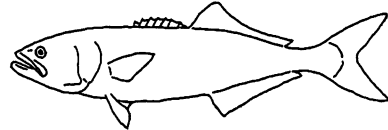
Branchiostegidae



Labracoglossidae



Lactariidae



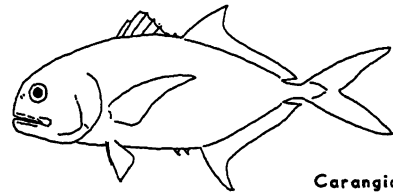
Pomatomidae



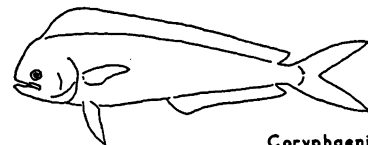
Rachycentridae



Echeneidae



Carangidae



Coryphaenidae

CHART 22.

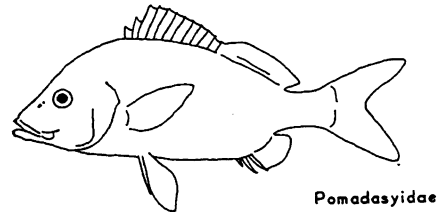
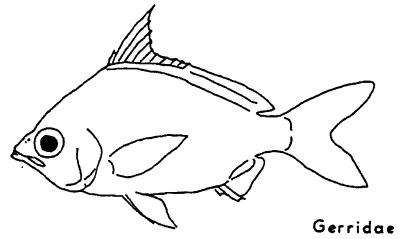
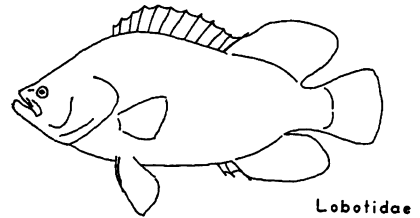
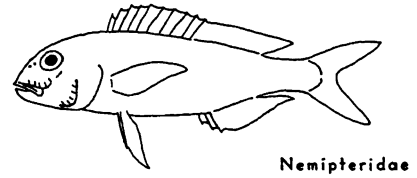
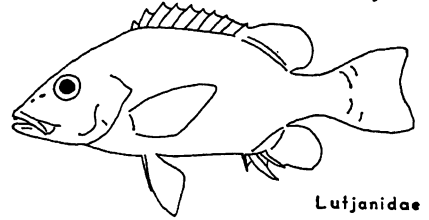
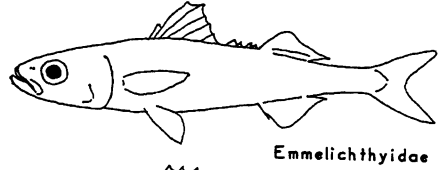
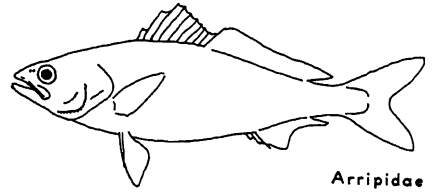
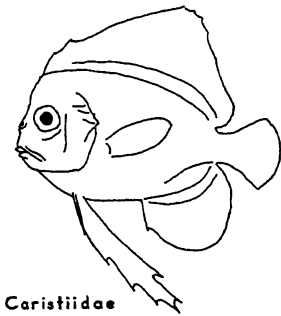
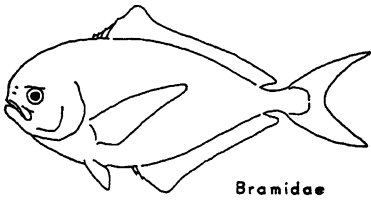
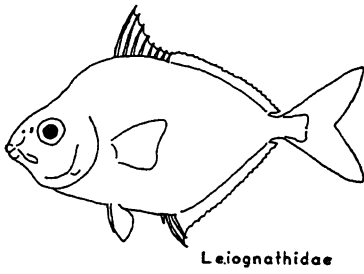
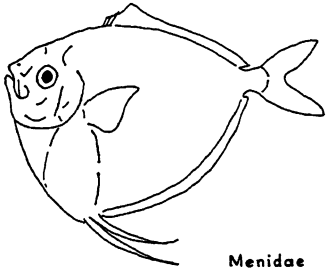
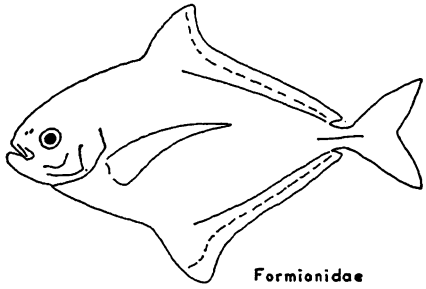
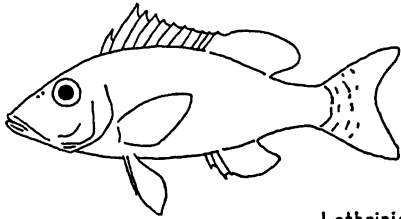
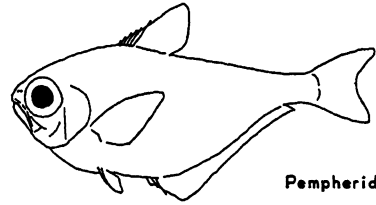


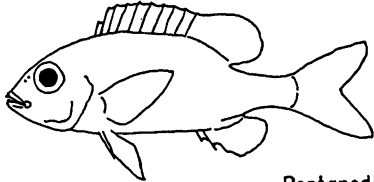
CHART 23.



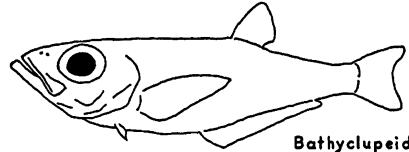
Lethrinidae



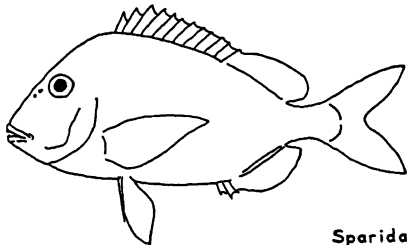
Pempheridae



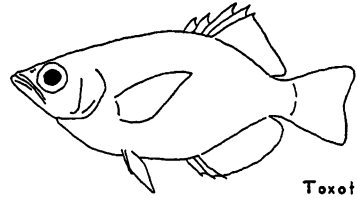
Pentapodidae



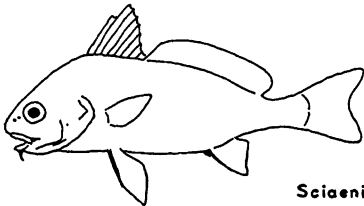
Bathyclupeidae



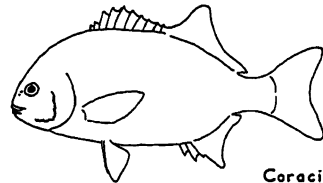
Sparidae



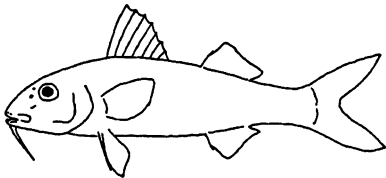
Toxotidae



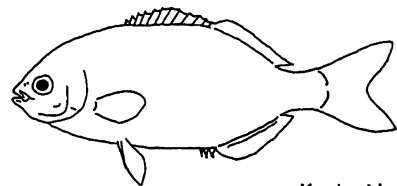
Sciaenidae



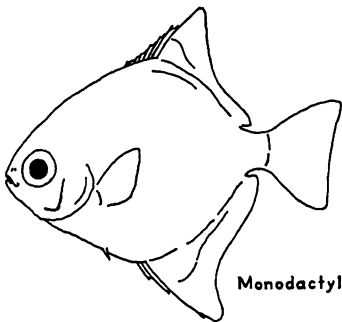
Coracinae



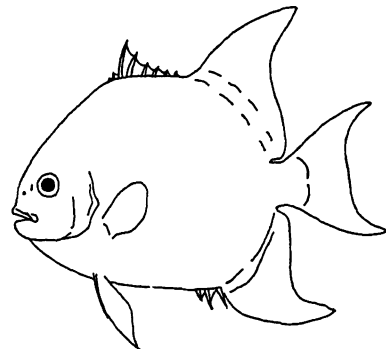
Mullidae



Kyphosidae

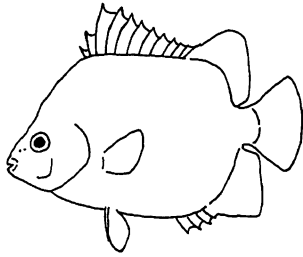


Monodactylidae

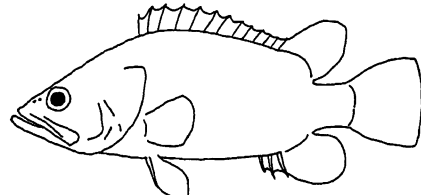


Ephippidae

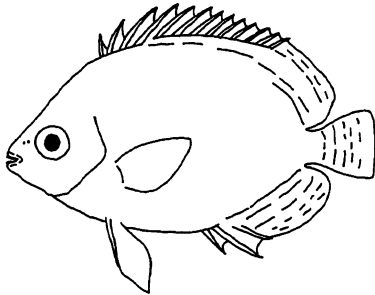
CHART 24.



Scatophagidae



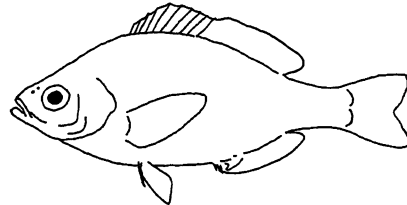
Nandidae



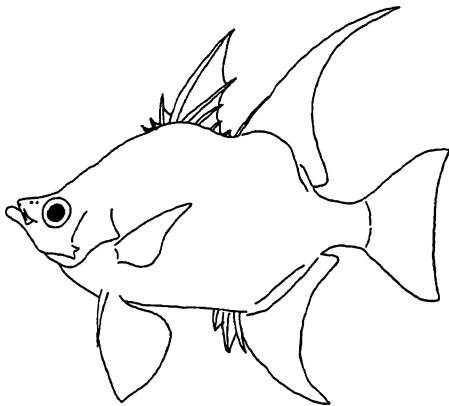
Chaetodontidae



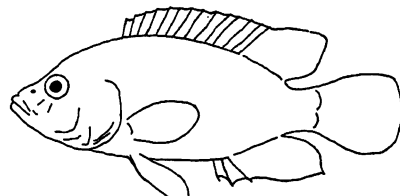
Oplegnathidae



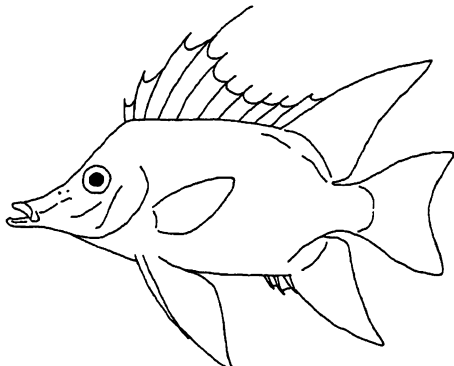
Embiotocidae



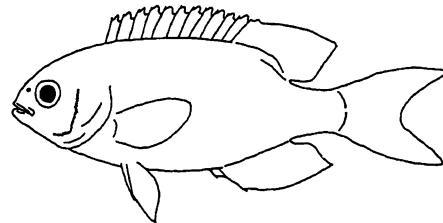
Enoplosidae



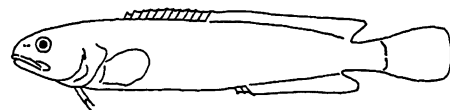
Cichlidae



Pentacerotidae

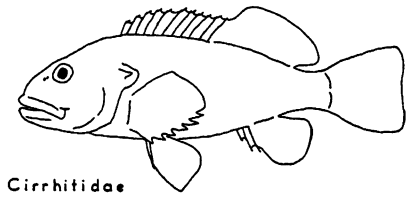


Pomacentridae

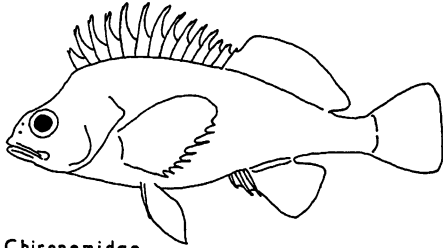


Gadopsidae

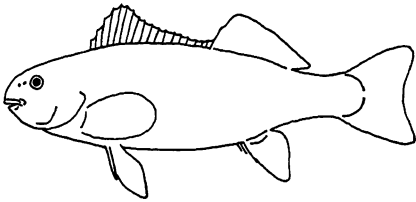
CHART 25.



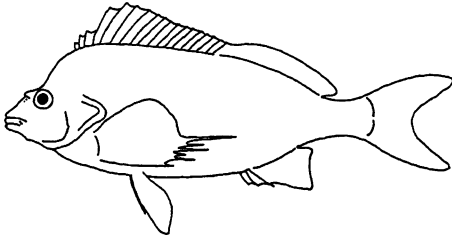
Cirrhitidae



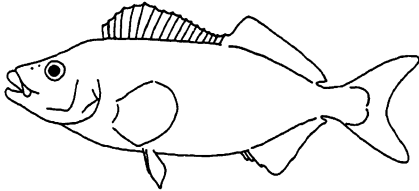
Chironemidae



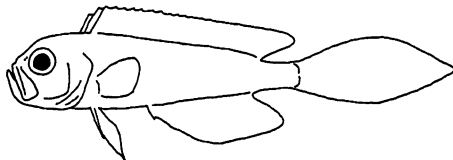
Aplodactylidae



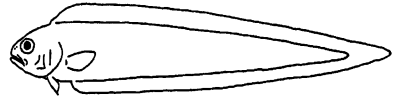
Cheilodactylidae



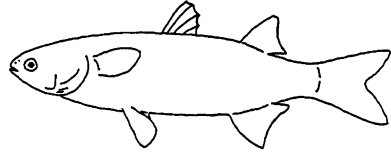
Latridae



Owstoniidae



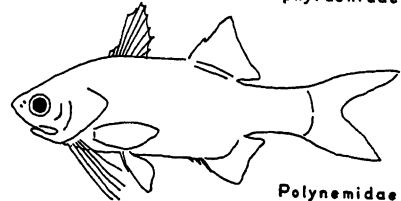
Cepolidae



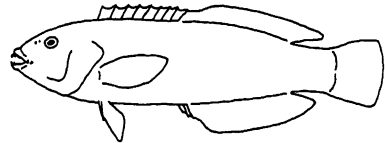
Mugilidae



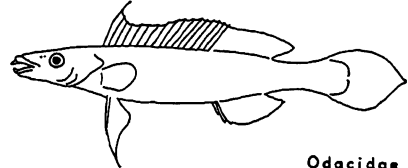
Sphyraenidae



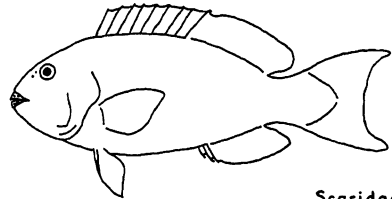
Polynemidae



Labridae



Odacidae

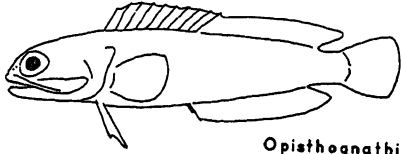


Scaridae

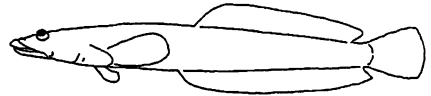


Trichodontidae

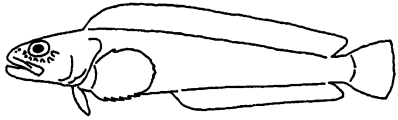
CHART 26.



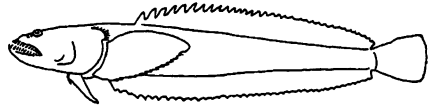
Opisthognathidae



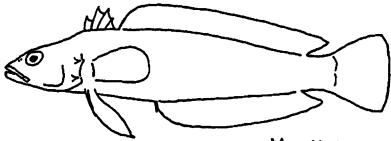
Limnichthyidae



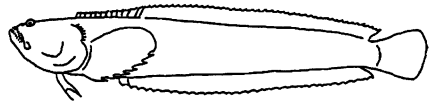
Bathymasteridae



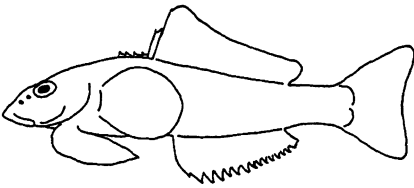
Leptoscopidae



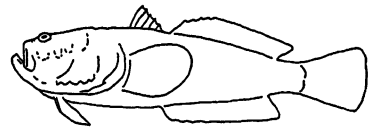
Mugiloididae



Dactyloscopidae



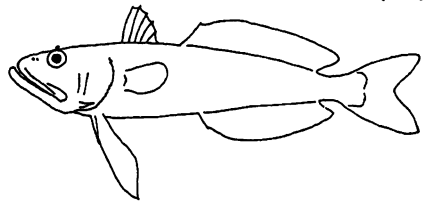
Cheimarrichthyidae



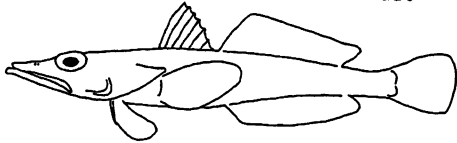
Uranoscopidae



Trachinidae



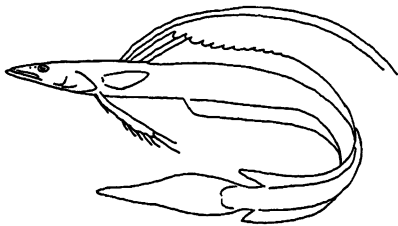
Champsodontidae



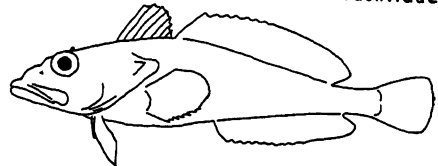
Percophididae



Chiasmodontidae



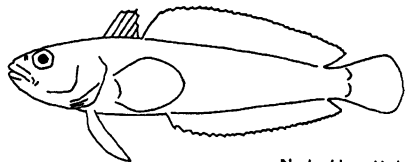
Trichonotidae



Bovichthyidae

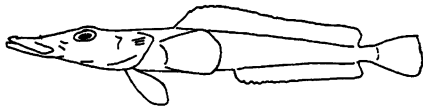


Creediidae

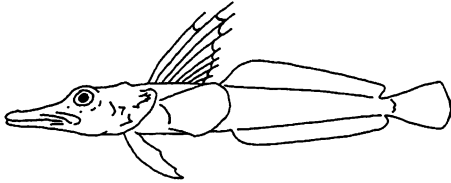


Nototheniidae

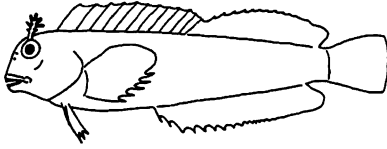
CHART 27.



Bathyaconidae



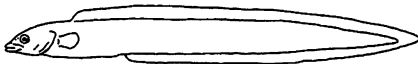
Channichthyidae



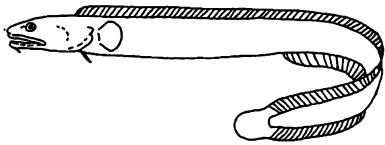
Blenniidae



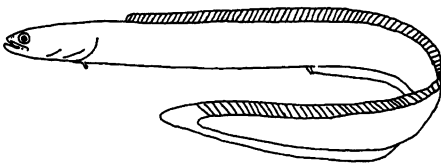
Anarhichadidae



Congrogadidae



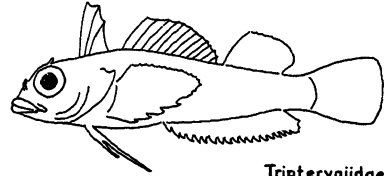
Notograptidae



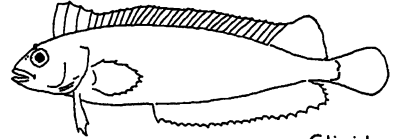
Peronedysidae



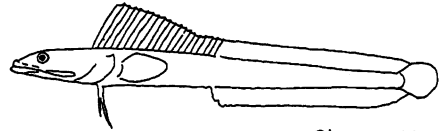
Ophioclinidae



Tripterygiidae



Clinidae



Chaenopsidae



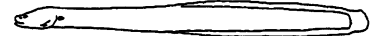
Stichaeidae



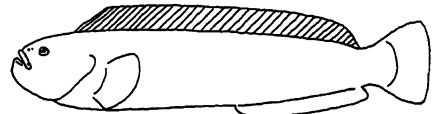
Ptilichthyidae



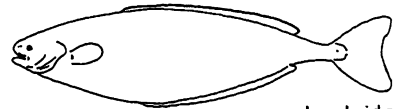
Pholididae



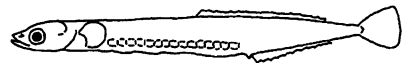
Scytalinidae



Zaproridae

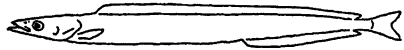


Icosteidae

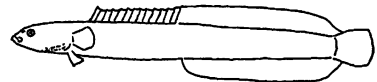


Schindleriidae

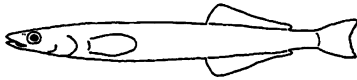
CHART 28.



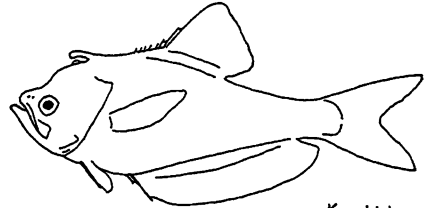
Ammodytidae



Microdesmidae



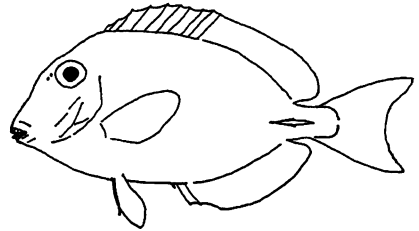
Hypoptychidae



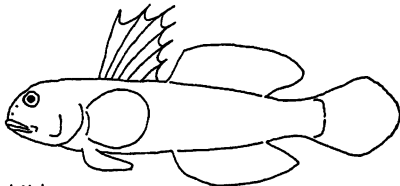
Kurtidae



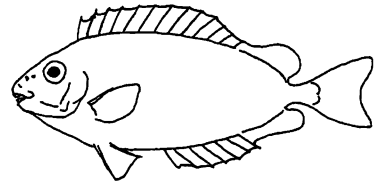
Callionymidae



Acanthuridae



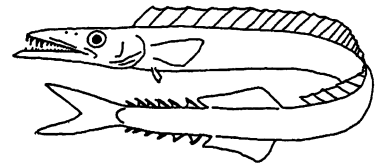
Gobiidae



Siganidae



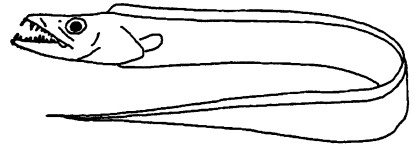
Rhyacichthyidae



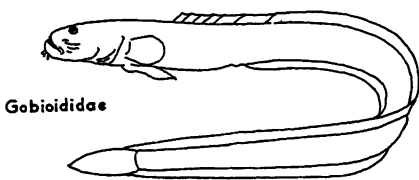
Gempyliidae



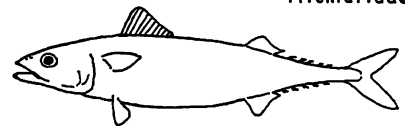
Kraemeriidae



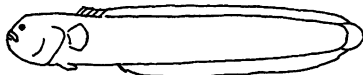
Trichiuridae



Gobioididae

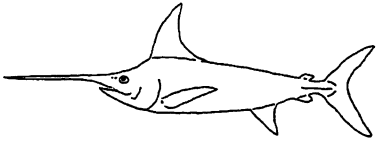


Scombridae

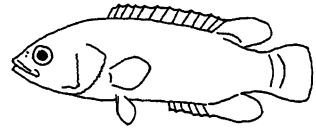


Trypauchenidae

CHART 29.



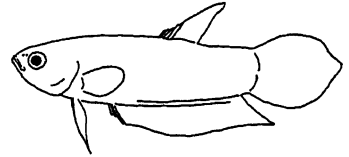
Xiphiidae



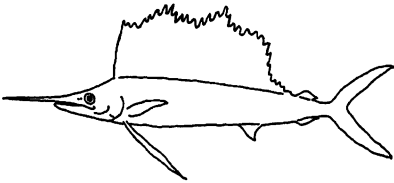
Anabantidae



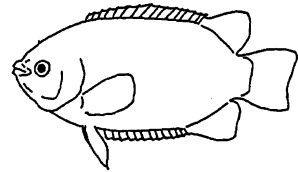
Luvaridae



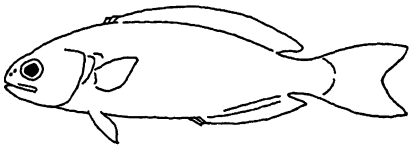
Belontiidae



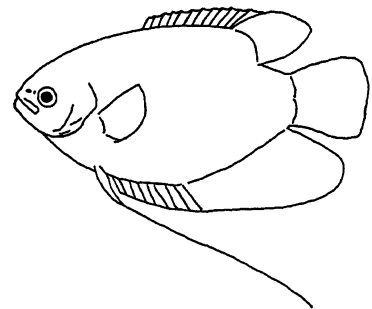
Istiophoridae



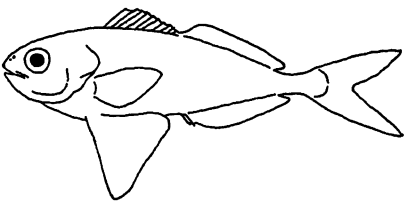
Helostomatidae



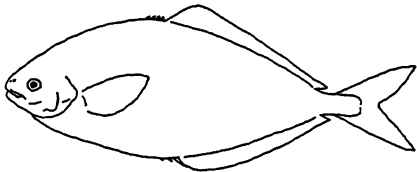
Centrolophidae



Osphronemidae



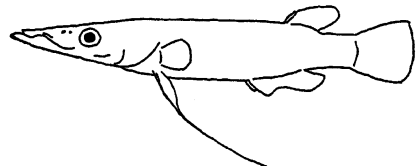
Nomeidae



Stromateidae

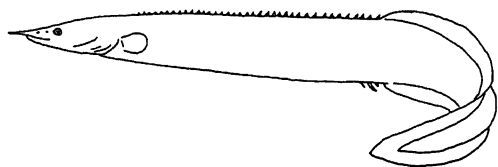


Tetragonuridae

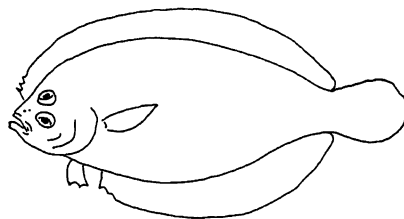


Luciocephalidae

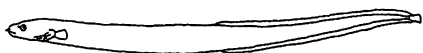
CHART 30.



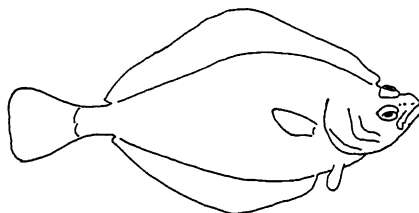
Mastacembelidae



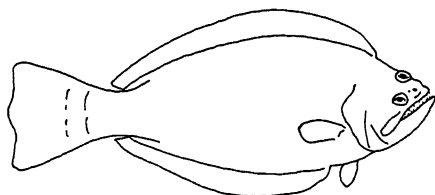
Bothidae



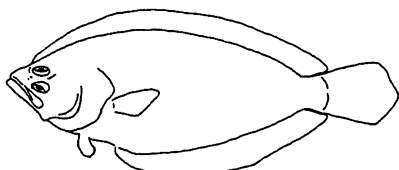
Chaudhuriidae



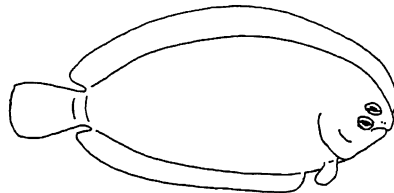
Pleuronectidae



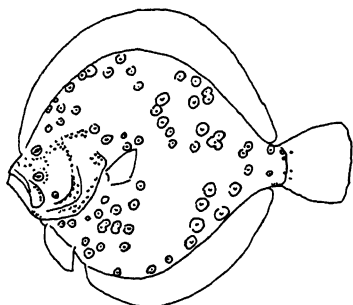
Psettodidae



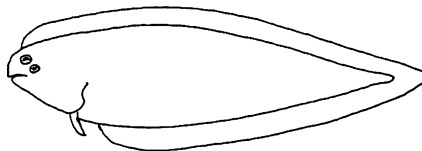
Citharidae



Soleidae

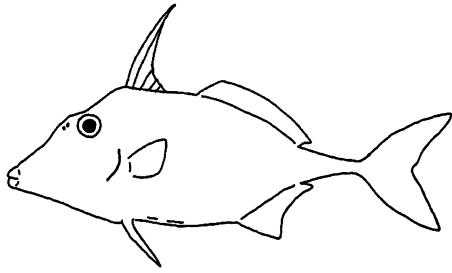


Scophthalmidae

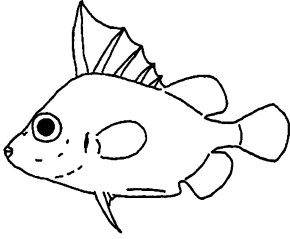


Cynoglossidae

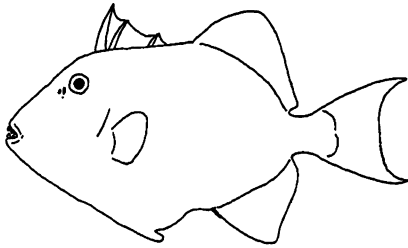
CHART 31.



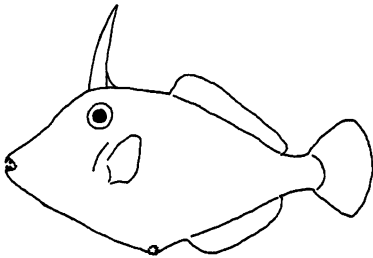
Triacanthidae



Triacanthidae



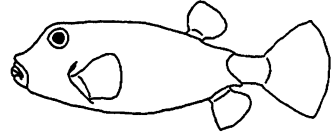
Balistidae



Balistidae



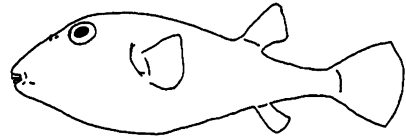
Balistidae



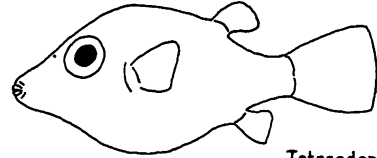
Ostraciontidae



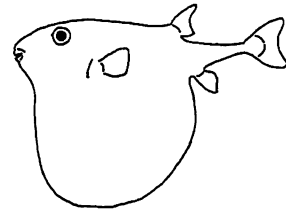
Ostraciontidae



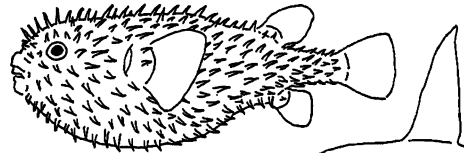
Tetraodontidae



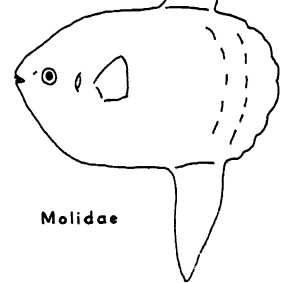
Tetraodontidae



Triodontidae



Diodontidae



Molidae

CHART 32.

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